STUDIES ON HUMAN VISIBLE PERSISTENCE

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Abstract

The visual system has limited temporal resolution, with the intensity of brief stimulus presentations being summed, or integrated over time. This temporal integration may manifest itself in various ways, including time-intensity reciprocity at threshold (Bloch's Law), flicker fusion, some masking phenomena, and visible persistence. The degree of visual temporal resolution varies with a number of conditions, including luminance, field size, and the spatial frequency of gratings. Many of these temporal properties may possibly be explained in terms of interactions between two parallel visual mechanisms - "sustained" and "transient" channels. These appear to analyse pattern and movement respectively.

This thesis reports investigations into properties of one of these temporal characteristics, visible persistence. It attempts to relate persistence to threshold measures of temporal summation, especially time-intensity reciprocity. It is argued that persistence may occur at more than one level of the visual system and that the more peripheral component may result from processes similar to those responsible for the "critical duration" of time-intensity reciprocity.

Using a separation threshold method, persistence duration was found to increase with both increasing spatial frequency and decreasing contrast. By measuring persistence over several stimulus durations it was possible to show that it consisted of two components. One occurred only at brief

stimulus durations and declined linearly with increasing stimulus duration. The other appeared to be present and approximately constant at every stimulus duration. Varying stimulus conditions such as orientation, contrast and spatial frequency affected these components differently. These effects were consistent with the hypothesis that one component is peripherally located and the other more central.

It was argued that persistence at both levels is due to the prolonged nature of sustained cell responses, with high frequency gratings stimulating mechanisms with longer response durations than the mechanisms stimulated by low frequency gratings. It was also proposed that response duration may be influenced by the amplitude or latency of transient mechanisms but neither flicker adaptation nor reaction time experiments supported this.

It was noted that the conditions which elevate persistence such as the use of higher spatial frequencies, oblique orientations and lower contrast levels would all be expected to produce weaker neural stimulation. It appears therefore that for weaker neural stimulation the response duration is lengthened, as if in compensation.

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I would finally like to thank all my friends for their encouragement and support throughout the project.

Sources Statement

The present thesis describes original research undertaken in the Department of Psychology, University of Tasmania. To the best of my knowledge and belief, any theories and techniques not my own have been acknowledged in the text. The theoretical contributions in this thesis are my own original work and have not been submitted for any other degree.

Signed ..Alison..Bowling.....

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CHAPTER 1

SPATIAL AND TEMPORAL ANALYSIS IN THE VISUAL SYSTEM

1.00 General introduction

The visual systems of humans and higher animals are comprised of complex networks of neurones which analyse a retinal image to produce a percept of the visual input. Neurones within this network are specialised to respond to specific stimulus properties. Processing commences at the level of the retinal ganglion cells and continues through the lateral geniculate nucleus to the visual cortex. Specialized cells occur at each level of processing culminating in the cortex where neurones responsive to features such as orientation, length, direction of movement, velocity, spatial frequency, colour and other stimulus properties have been identified in higher mammals (e.g. Hubel & Wiesel, 1962; 1968; Orban & Callens, 1977; Schiller, Finlay & Volman, 1976a, b, c).

Spatial and temporal information appear to be processed in parallel systems of cells (Stone, Dreher & Leventhal 1979), temporal information being transmitted by a group of short-latency, fast-responding neurones (Y cells), and spatial information by a group of longer latency neurones with sustained responses (X cells). Specialized cells are found in both systems, although the areas of specialization may differ between the systems and some stimulus features are predominantly processed by cells belonging to only one system (Dow, 1974; Gouras, 1969). Cells of the X system

possess a greater degree of specificity to spatial variables than do cells of the Y system, which respond more actively to movement or flicker (Ikeda & Wright, 1975a, b; Maffei, 1978; Movshon, Thompson & Tolhurst, 1978; Stone & Dreher, 1973). Although there may be some degree of overlap between the spatial sensitivities of the two groups of cells (e.g. Lehmkuhle, Kratz, Mangel & Sherman, 1980), it appears that pattern analysis is performed predominantly by the X system. The properties of the X and Y systems will be described in more detail in later sections of this chapter.

1.10 Pattern analysis

A theory which has generated much research in recent years is that the visual system performs a Fourier or spatial frequency analysis of the input luminance distribution. It is hypothesised that a complex stimulus is analysed into its component sinusoidal luminance distributions, rather than into its edge, length and other features (De Valois & De Valois, 1980). The visual system is thought to contain spatial filters which are sensitive to limited frequency ranges of these distributions. The simplest stimulus to which the visual system responds is thus considered to be a sinusoidal grating, since all complex luminance distributions can be decomposed into these by Fourier analysis.

To be able to perform such an analysis, the visual system requires mechanisms that respond only to limited spatial frequency ranges. Evidence for the existence of spatial frequency specific cells in animals, and for human spatial frequency specific visual channels follows.

1.11 Electrophysiological studies of pattern detecting mechanisms

Hubel and Wiesel (1962) provided a major insight into pattern vision by their demonstration that cells of the cat visual cortex were maximally responsive to lines or edges of a specific orientation, rather than to spots of light. Three types of cortical cell were identified. Simple cells had elongated receptive fields with laterally organised excitatory and inhibitory regions accounting for their orientation specificity. In comparison, the receptive fields of complex cells were not subdivided into obvious excitatory and inhibitory areas but the cell responded to a correctly oriented bar or edge falling anywhere in the receptive field. Hypercomplex cells possessed both orientation and length specificity with their receptive fields having inhibitory regions at each end.

Hubel and Wiesel (1962) proposed that these cells were hierarchically organised. Simple cells were considered to receive excitatory input from a number of lateral geniculate cells in such a way that adjacent circular receptive fields of these cells combined to produce the elongated simple cell receptive field. It was additionally proposed that complex cells received input from a number of simple cells, and hypercomplex cells from a number of complex cells. This hierarchical model has recently been challenged, however, by the discovery of apparently parallel X and Y cell systems (Stone et al. 1979).

Enroth-Cugell and Robson (1966) first demonstrated spatial frequency specificity in retinal ganglion cells of the cat.

Each cell responded to a limited range of spatial frequencies with the optimal spatial frequency varying from cell to cell. Cells of the lateral geniculate nucleus and striate cortex also respond selectively to limited ranges of spatial frequency (Cambell, Cooper & Enroth-Cugell, 1969; Maffei & Fiorentini, 1973). A progressive narrowing of the spatial frequency tuning from retinal ganglion to simple cortical cells was found to occur (Maffei & Fiorentini, 1973). Maffei and Fiorentini also found that simple cells were more narrowly tuned than complex cells, although this finding has not always been replicated (Ikeda & Wright, 1975a; Movshon et al., 1978). Cells responsive to limited ranges of spatial frequency have also been observed in monkey visual systems (Campbell, Cooper, Robson & Sachs, 1969; Schiller et al., 1976c). The optimal spatial frequency of a cell depends to some extent upon the size of the receptive field centre, with receptive field size being correlated with spatial resolution (Cleland, Harding & Tulunay-Keesey, 1979; Maffei & Fiorentini, 1977). This correlation is not always strong, however, and the spatial frequency sensitivity of a cell cannot necessarily be predicted from its receptive field size (Lehmkuhle et al., 1980).

Simple cells of the striate cortex are the most narrowly tuned to spatial frequency and also possess a number of other characteristics which may enable them to behave as spatial filters (Maffei, 1978). They are generally more narrowly tuned to orientation than complex cells and show an optimum response when the stimulus is an extensive grating rather than one comprising just a few bars. They are sensitive to spatial phase and contrast and are affected

by adaptation, unlike retinal ganglion, geniculate and most complex cells (Maffei, 1978). Maffei argues that these cells have all the characteristics necessary for them to perform a spatial frequency analysis.

Other investigators have argued that complex rather than simple cells are more likely to be spatial frequency analysers since, if the hierarchical model is valid, these cells derive input from several simple cells. Their receptive fields may consequently contain several parallel inhibitory and excitatory bands. Glezer, Ivanoff and Tscherbach (1973) found that complex cells in the cat visual cortex responded best to stimuli comprised of two or more slits of light. Pollen and Ronner (1975) obtained evidence for the existence of multi-peaked receptive field profiles which would respond optimally to a single preferred spatial frequency. Pollen and Taylor (1973) and Pollen, Lee and Taylor (1971) have proposed that these spatial frequency and orientation selective complex cells have all the requirements for them to perform a two-dimensional frequency transformation of a stimulus.

To investigate the capacity of cells of the striate cortex of cats and monkeys to behave as spatial frequency filters De Valois, De Valois and Yund (1979) compared the responses of these cells to gratings and checkerboards. It was found that the orientation and spatial frequency tuning of both simple and complex cells were predictable from the Fourier components of the checkerboards rather than from the check size and orientation. Furthermore, it was found that these cells responded to the third harmonic of square wave gratings

and checkerboards, and that their orientation tuning was predictable from the orientation of the third Fourier harmonic of checkerboards, rather than from the orientation of the edges. These data indicate that both simple and complex cells of area 17 may perform a spatial frequency analysis.

The current evidence thus favours the hypothesis that, in the cat, pattern analysis is predominantly carried out by simple (and some complex) cortical neurones narrowly tuned to spatial frequency and located in area 17. Populations of these cells have been shown to vary systematically in the optimal spatial frequency to which they are sensitive (Maffei & Fiorentini, 1977). These cells perform the pattern analysis by breaking down the input luminance distribution into its component spatial frequencies.

This physiological evidence for spatial frequency specific neurones in cats and monkeys has been compared with psychophysical evidence indicating that similar pattern analysing mechanisms exist in man. A brief outline of this evidence follows.

1.12 Psychophysical evidence for spatial frequency analysis

The impetus for psychophysical research into the spatial frequency analysis theory was provided by Campbell and Robson (1968). They demonstrated that, over a wide range of spatial frequencies, the contrast threshold of a non-sinusoidal grating (e.g. one with a square or triangular wave luminance distribution) was determined only by the amplitude of its fundamental Fourier component. They also showed that these gratings cannot be distinguished from

sine-wave gratings at low contrast levels. High contrast levels are necessary for the higher harmonic components, which provide edge and other information about detail, to be above threshold. It was concluded that the visual system contains narrow-band spatial filters which respond independently to the different Fourier components of the gratings. Similar results have been obtained with more complex patterns (e.g. Kelly, 1976; Kelly & Magnuski, 1975).

Subsequent work using adaptation paradigms confirmed that visual mechanisms are responsive to limited spatial frequency ranges (e.g. Blakemore & Campbell, 1969; Blakemore, Nachmias & Sutton, 1969). Blakemore and Campbell showed that adaptation to a grating of a particular spatial frequency elevated the contrast thresholds of subsequently presented gratings within about an octave of the adapting frequency. No contrast threshold elevation was observed at frequencies beyond this. The bandwidth of the spatial filters was thus approximately one octave. Adaptation and masking procedures have been used to provide evidence that non-periodic stimuli such as single bars and dots are also analysed by the visual system into their component spatial frequencies (Sullivan, Georgeson & Oatley, 1972; Weistein & Bisaha, 1972; Weisstein, Harris, Kerbaum, Tangney & Williams, 1977). A considerable amount of evidence in favour of spatial frequency analysis has accumulated (De Valois & De Valois, 1980).

To test whether the spatial frequency, or the alternative feature detection model (e.g. Barlow, 1972) is the most appropriate theory of pattern analysis, researchers have

employed stimuli in which some characteristic of the major features (bars or edges) differs from that of the fundamental Fourier components. Checkerboards are particularly useful since the orientations of the edges and Fourier components differ by 45^{o}. Several studies have shown that the analysis of these stimuli is consistent with the spatial frequency model (Green, Corwin & Zemon, 1976; Kelly, 1976; Lovegrove, Bowling & Gannon, Note 1; May & Matteson, 1976). For example, Green et al. (1976) and May and Matteson (1976) demonstrated that colour contingent aftereffects are associated with the major Fourier components of the checkerboard, rather than with the edges of the checks.

Both electrophysiological and psychophysical research indicate that mechanisms in the visual systems of higher mammals and man are spatial frequency specific and that they may perform a spatial frequency analysis. Further research has shown that these mechanisms belong predominantly to the X-cell system. Recent evidence has indicated that another system of cells exists and that these Y-cells are specialised to analyse temporal information. The characteristics of these apparently parallel systems of cells will now be described.

1.20 Temporal analysis

1.21 The X/Y/W classification

Retinal ganglion cells with different response properties to sinusoidal gratings were originally described in cats by Enroth-Cugell and Robson (1966). For one group of cells (X-cells) it was possible to find a position of the grating

relative to the receptive field (the null position) where its introduction and withdrawal did not produce any response from the cell. These cells exhibited linear spatial summation over their receptive fields. The second group of cells (Y-cells) responded to the introduction and withdrawal of the grating with brief bursts of activity at the equivalent position to that producing no response in an X-cell. These cells thus exhibited non-linear spatial summation.

The two cell types have been extensively studied and have also been identified in the cat lateral geniculate nucleus (Cleland, Dubin & Levick, 1971; Derrington & Fuchs, 1979; Lehmkuhle et al., 1980). Cells with similar properties occur in the visual cortex (Ikeda & Wright, 1975a, b; Leventhal & Hirsch, 1977; Movshon et al., 1978). X-like and Y-like cells have been observed among retinal ganglion and lateral geniculate cells in monkeys (de Monasterio, 1978a, b; Dreher, Fukada & Rodieck, 1976; Gouras, 1969; Marrocco, 1976) and psychophysical studies have revealed that these cells may also occur in man (e.g. King-Smith & Kulikowski, 1975; Kulikowski & Tolhurst, 1973).

Correlations with morphological studies have revealed that Y cells have large cell bodies and sparsely branched dendrites and that X-cells are smaller, with more densely branched dendritic trees (Levick, 1975). Although most studies have concentrated on the differences between X- and Y-cells, it is now known that a third, heterogeneous group of cells exists, and that these make up a considerable proportion of retinal ganglion cells (Stone et al., 1979).

They have generally been classified as W cells, although Cleland and Levick (1974a, b) subdivide this group into "sluggish-sustained", "sluggish-transient" and non-concentric cells. All these cell types have small cell bodies. Little is known about their function, although Stone et al. (1979) have suggested that they may be involved in "ambient" vision which controls visual orienting responses, pupil contraction, reflex direction of gaze, and detection and tracking of objects.

1.22 Physiological properties of X- and Y-cells

The original classification of X- and Y-cells used linearity of spatial summation as the defining characteristic (Enroth-Cugell & Robson, 1966). The use of this characteristic has been extended by Hochstein and Shapley (1976) who obtained a measure of non-linearity (the non-linearity index) for each cell, and showed that, using this classification, there was no overlap between X- and Y-cells. In addition, the measure was invariant with temporal waveform, frequency and contrast of the stimulus, and with the eccentricity of the cell. Other investigators have used a number of different methods to classify retinal ganglion cells, including their response to a drifting grating (Enroth-Cugell & Robson, 1966; Cleland et al., 1971), to small spots of light (Cleland et al., 1971; Cleland, Levick & Sanderson, 1973; Ikeda & Wright, 1972a) and to diffuse light (Fukada, 1971). Based on their response to light flashes, the cells have been classified as "transient" or "sustained". At the onset of a spot of light centred in the receptive field, transient cells produce an initial burst

of impulses. This rapidly declines to the spontaneous level of the cell. Sustained cells produce a prolonged response while the stimulus is present (Cleland et al., 1971; Ikeda & Wright, 1972a). Increasing the diameter of the spot beyond the size of the receptive field centre causes an inhibition in the response of sustained cells but not necessarily in that of transient cells (Cleland et al., 1973; Ikeda & Wright, 1972a). Sustained cells thus respond optimally to small stimuli whereas transients may respond to flashes of any magnitude. Derrington & Fuchs (1979) and Ikeda & Wright (1972c) have shown that transient cells may also be affected by stimuli presented well away from the receptive field (periphery effect).

The sustained-transient and the X-Y classifications were originally thought to be identical (e.g. Cleland et al., 1971) since they have a number of common characteristics. Recent evidence has shown, however, that the sustained or transient nature of the response is not an invariant characteristic of a cell. Changes in adaptation level (Jakiela, Enroth-Cugell & Shapley, 1976), colour and intensity (de Monasterio, 1978a, b) may produce changes in the nature of the response. Differences in the type of response also occur with cell eccentricity. For example, Hochstein and Shapley (1976) identified a peripheral cell as an X-cell on the basis of its linear spatial summation. This cell, however, produced transient responses to flashing spots and diffuse light. It is possible that many similar peripheral X-cells have been identified as transients by investigators using response to standing contrast as the

basis of their classification. This may have given rise to the claim that transient cells predominate in the periphery and sustained cells in the area centralis (e.g. Cleland et al., 1971, 1973; Ikeda & Wright, 1972b). Using the index of linearity as the basis of classification, however, Hochstein and Shapley (1976) reported that the proportions of X- and Y-cells in the centre and periphery did not vary greatly. Cleland et al. (1979) and Peichl and Wassle (1979) have made similar observations, and these are in agreement with morphological studies (e.g. Boycott & Wassle, 1974).

The sustained-transient and X-Y classifications thus do not correspond exactly. The sustained-transient classification describes the nature of the cell response under a particular set of conditions whereas the X-Y classification describes the type of cell involved. Although the responsese of X-cells are frequently sustained and those of Y-cells transient, this is not always the case. The two response types are trends rather than invariant characteristics of X- and Y-cells (e.g. Derrington & Fuchs, 1979; Hochstein & Shapley, 1976).

Characteristics of X- and Y-cells which are dependent upon the degree of linearity of the receptive field are their responses to flickering and drifting gratings (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976; de Monasterio, 1978a). An X-cell will respond to a flickering grating by a sinusoidal modulation of its response rate for all spatial frequencies to which it is sensitive. A Y-cell responds to low spatial frequencies similarly, except when the grating is in the null position. In that case a frequency doubling of the cell response rate occurs. This

frequency doubling occurs at all grating positions when high spatial frequency gratings are employed. The Y-cell thus gives an "on-off" response to each phase of grating alternation. Y-cells consequently have two types of response to flickering gratings - a modulation of their response rate to low frequency gratings, and "on-off" responses to high frequency gratings. Further evidence for two response mechanisms in Y-cells is obtained when the stimuli are drifting gratings. In this case an X-cell produces a response modulated about the mean. Y-cells also respond with a modulated response to low frequency gratings but the mean response rate of the cell also increases. With higher spatial frequencies, the modulated response does not occur but the cells continue to respond with an increase in their mean discharge rate. The spatial contrast sensitivity of Y-cells can thus be measured in two ways; (1) by considering only the modulated response of the cell, and (2) by investigating the total range of frequencies to which the cell responds with either a modulated or unmodulated increase in its mean firing rate. When method (2) is employed Y-cells may not differ greatly from X-cells in the maximum spatial frequencies to which they are sensitive (e.g. Lehmkuhle et al., 1980). When only the spatial frequency resolution of the unmodulated response is considered, however, Y-cells have lower cut-off frequencies than X-cells and there is no overlap in sensitivities at any one retinal eccentricity (Cleland et al., 1979). X-cells also show a low frequency attenuation of the contrast sensitivity function, and thus, narrower tuning than Y-cells (Derrington & Fuchs, 1979; Enroth-Cugell & Robson,

1966; Maffei & Fiorentini, 1973). It is possible that the two response characteristics of Y-cells may allow them to process low frequency pattern information, as well as to signal onset, offset and movement at much higher spatial frequencies.

X- and Y-cells differ in their temporal as well as in their spatial properties. Y-cells tend to have shorter response latencies (de Monasterio, 1978a; Dreher et al., 1976) and faster conduction velocities (Cleland et al., 1971; Fukada, 1971; Gouras, 1969; Hoffman & Stone, 1971; Ikeda & Wright, 1972a) giving them greater temporal resolution than X-cells (Fukada & Saito, 1971; Lehmkuhle et al., 1980; Orban & Callens, 1977). In cat optic nerves temporal contrast sensitivity functions of Y-cells were found to have both a low and high frequency fall off, while X-cells had neither (Fukada & Saito, 1971). In geniculate cells, however, Derrington and Fuchs (1979) and Lehmkuhle et al. (1980) failed to find a low frequency attenuation in Y-cells, although these tended to resolve higher temporal frequencies than X-cells. In the cat visual cortex Ikeda and Wright (1975a) and Movshon et al. (1978) found that the temporal frequency tuning curves of "sustained" cells had shallow or flat low frequency response characteristics. "Transient" cells, however, frequently had a pronounced low temporal frequency cut. Y-like cells at this level of the visual system thus showed finer temporal tuning than X-like cells. It is possible that temporal tuning in Y-cells becomes progressively sharper from the retina to visual cortex in a similar manner to that observed for spatial tuning in X-cells (e.g. Maffei & Fiorentini, 1973).

A further difference in the response properties of the two cell types may be obtained using repeated presentations of very brief pulses of light (Cleland et al., 1973). X-cells were shown to produce responses that were much more prolonged than those of Y-cells. These prolonged responses to very brief stimuli may account for temporal integration (Levick & Zacks, 1970) and persistence (Breitmeyer & Ganz, 1976) as is discussed more fully in chapters 2 and 3.

X-cells have been shown to project primarily to area 17 of the cat visual cortex whereas individual Y-cells may project to both areas 17 and 18 by means of a branching axon (Stone & Dreher, 1973). The simple (and complex) cells of area 17 are similar in many ways to X-cells, whereas complex cells of area 18 are similar to Y-cells (Stone & Dreher, 1973; Stone et al., 1979). Area 17, comprising mainly X-like cells (Movshon et al., 1978) which may behave as spatial filters (De Valois et al., 1979) appears to be specialized for pattern analysis, and area 18, with velocity-tuned Y-like cells responding to fast movement (Orban & Callens, 1977) has the necessary requirements for temporal analysis.

1.23 Psychophysical studies of sustained and transient mechanisms

There is a considerable volume of literature relating visual spatial and temporal processing in man to X- and Y-cell properties. The mechanisms inferred from psychophysics deal mainly with the sustained and transient nature of visual responses and their spatio-temporal properties rather

than with the linearity or otherwise of spatial summation (with the exception of a study by King-Smith and Kulikowski, 1975). The sustained-transient nomenclature will consequently be used to refer to the mechanisms inferred from psychophysical studies. This is to maintain the distinction between X- and Y-cells, and sustained and transient responses referred to previously.

Much of the psychophysical evidence for the existence of sustained and transient mechanisms in man has been recently summarised by Legge (1978). Only those studies most relevant to the present thesis will be discussed here.

Several investigations have indicated that humans have separate contrast thresholds for detection of pattern and flicker. It has been inferred from these that separate pattern and flicker detectors exist (Keesey, 1972; Kulikowski, 1971; Kulikowski & Tolhurst, 1973; King-Smith & Kulikowski, 1975). Flicker detectors respond best to low spatial frequencies, and medium and high temporal frequencies. The temporal contrast sensitivity functions of these detectors have a pronounced low frequency attenuation. Pattern detectors are responsive to high spatial frequencies and to stationary or slowly flickered gratings.

Using a sub-threshold summation technique, King-Smith and Kulikowski (1975) were able to infer some of the receptive field properties of these detectors. The pattern detector showed linear spatial summation of contrast but the flicker detector was non-linear. In addition the flicker detector appeared to have a much broader receptive field than the pattern detector and showed variation in

receptive field properties with changes in stimulation which the pattern detector did not. These receptive field properties are similar to the properties of Y- and X-cells respectively.

That the pattern and flicker detectors are in fact separate mechanisms has been demonstrated recently by Bodis-Wollner and Hendley (1979). These experimenters used a test stimulus comprised of a steady grating and a superimposed counterphase flickering grating of the same spatial frequency and phase. The contrast modulation sensitivity was measured for a range of mean contrast levels and spatial frequencies both before and after adaptation to steady gratings of the same spatial frequency as the test stimulus. Adaptation to a high contrast steady grating unmasked the counterphase component of the test grating so that its threshold became independent of the contrast of the steady component. The data indicate that the pattern and flicker detectors are separate mechanisms since adaptation should suppress both detectors similarly if the same underlying mechanism was responsible for each.

The finding that, in cats, Y (transient) cells respond to lower spatial frequencies than X (sustained) cells has been used in a number of psychophysical experiments aimed at identifying similar mechanisms in man. Transient mechanisms in cats have been shown to produce "on" and "off" responses to the introduction and withdrawal of a grating, whereas sustained cells have a more prolonged response (Enroth-Cugell & Robson, 1966). Similar "transient" and "sustained" responses to gratings have been shown to occur in man. Furthermore, they depend upon the spatial frequency

of the grating. Tolhurst (1975a) measured reaction times to grating stimuli at approximately threshold contrast. Low spatial frequency gratings were found to be detected at the (abrupt) onset or offset of the grating, while high frequency gratings were detected throughout the duration of the stimulus. In addition, a low frequency subthreshold grating was found to facilitate the detection of a brief test grating of the same spatial frequency only briefly after the onset or the offset of the subthreshold stimulus (Tolhurst, 1975b). Detection of a high frequency grating, however, was facilitated throughout the duration of the subthreshold pattern. Mechanisms responsive to low spatial frequencies thus give transient step-responses (at threshold) whereas those responsive to higher frequencies have sustained responses. Similar data to those obtained by Tolhurst (1975a) have recently been obtained in rhesus monkeys by Harwerth, Boltz and Smith (1980). These data, together with data obtained by Harwerth and Levi (1978) and Legge (1978) also indicate that sustained mechanisms are responsible for the threshold detection of pulsed gratings for all except low spatial frequencies (less than 1 c/deg.). It must be pointed out, however, that in these experiments separate mechanisms have not necessarily been identified, since it is quite possible that the response properties of the same mechanism vary with changes in spatial frequency.

It has been repeatedly demonstrated that the conduction velocity and response latency of Y-cells is faster than that of X-cells (e.g. Cleland et al., 1971, 1973). Since X-cells respond to higher spatial frequencies than Y-cells, it would be expected that higher spatial frequency information

would be transmitted more slowly than that of lower spatial frequencies. This has been demonstrated in man using a reaction time technique (Brietmeyer, 1975a; Lupp, Hauske & Wolf, 1976; Vassilev & Mitov, 1976). The latency of the early components of the visual evoked potential (VEP) has also been shown to increase with increasing spatial frequency (Parker & Salzen, 1977; Vassilev & Strashimirov, 1979), and a similar result was obtained for the latency of the neuromagnetic response (Williamson, Kaufman & Brenner, 1978). In many of these studies the gratings were equal in apparent contrast so that the latency effect was clearly due to the spatial frequency differences rather than to any differences in apparent contrast. Although this result has been interpreted as evidence for the activity of transient and sustained mechanisms at low and high frequencies respectively, it also may result from a spatial frequency related decline in conduction speeds within the sustained system alone.

Harwerth and Levi (1978) have investigated this issue further by measuring the reaction times to a range of contrast levels at each spatial frequency. When reaction time was plotted against contrast, a discontinuity in the relationship was observed for a wide range of intermediate spatial frequencies. They argued that reaction time was determined by the activities of two separate mechanisms: sustained at low contrast levels, and transient at high. The sustained contribution appeared to increase with increasing spatial frequency. A similar result has been obtained in monkeys (Harwerth et al., 1980). These data indicate that at suprathreshold contrast levels, transient mechanisms may

respond to high as well as to low spatial frequencies.

These data may be compared with VEP data of Kulikowski (1977a). At high contrast levels the VEP comprised both short latency early components (possibly transients) and late components with more prolonged activity (possibly sustained responses). With a decrease in contrast the latency of all components increased and their amplitude declined, but with high spatial frequency stimuli, the early components disappeared from the VEP at higher contrast levels than did the late components. The disappearance of the late components was shown to correlate with the psychophysically determined threshold contrast. If these late components do reflect sustained activity, the data indicate that, at intermediate and high spatial frequencies, sustained mechanisms determine threshold contrast, and that transient mechanisms become increasingly active at higher contrast levels. Kulikowski's data also show that transient mechanisms may determine threshold with very brief stimulus presentations.

Other research also leads to the conclusion that both transient and sustained mechanisms may respond to the same stimulus for a considerable range of spatial frequencies and contrast levels (e.g. Legge, 1978; Tolhurst, 1975a, b). It is probable that, at suprathreshold contrast levels, transient mechanisms produce on- and off-responses to the onset and offset of a stimulus while sustained mechanisms simultaneously produce a prolonged response. For example, with spatial frequencies less than 1 c/deg., transient mechanisms determine detection threshold. If these are

masked by high contrast pulses, detection threshold may be determined by sustained mechanisms alone (Legge, 1978).

In addition to their shorter latency, there is evidence that the duration of transient cell responses is shorter than sustained cell responses (Cleland et al., 1973). The response duration of a cell may determine the duration of temporal integration for the stimuli to which it is sensitive (Breitmeyer & Ganz, 1976). The critical duration (the time over which threshold contrast and stimulus duration are reciprocally related) is a measure of temporal integration. This increases with increasing spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978). This increase may reflect a change-over from predominantly transient mechanisms to predominantly sustained mechanisms with increasing spatial frequency.

If two brief pulses of the same stimulus are separated by an inter-stimulus interval (ISI), they interact in a manner which depends upon the duration of the ISI. Summation of the two responses occurs at brief ISI's but inhibition may occur at longer intervals (e.g. Ikeda, 1965). The resulting relationship between detection threshold and ISI is known as the summation function. Breitmeyer and Ganz (1977) and Watson and Nachmias (1977) found that gratings of low and intermediate spatial frequencies produce summation functions with a pronounced negative phase, indicating the presence of an inhibitory interaction between the two grating pulses. The interaction between gratings of higher spatial frequency lacked this inhibitory phase and showed summation over a longer time interval than occured for low spatial frequencies. A brief presentation of a low

spatial frequency grating therefore inhibits the response to a second grating if this occurs about 30-100 msec subsequently. The responses to the high frequency gratings, however, summate if they are separated by ISI's of up to 80 msec. It was inferred that this difference between summation functions was due to differences in the impulse responses of transient and sustained mechanisms, transients producing a response characterised by an inhibitory phase, and sustained mechanisms producing one without. Watson and Nachmias (1977) noted that the shape of the summation function changed gradually with increasing spatial frequency, indicating that a shift in the predominant response mechanism from transient to sustained occurred with increasing spatial frequency. The contributions of transient and sustained mechanisms to various spatio-temporal properties of vision will be considered further in chapter 3.

The data of Breitmeyer and Ganz (1977) and Watson and Nachmias (1977) indicate that activation of a transient mechanism may have a pronounced inhibitory effect on the transient response to a subsequently presented stimulus. Sustained mechanisms do not appear to have the same mutual inhibitory effect. Two stimuli may consequently interact differently depending upon their spatial frequency content. These results may be relevant for the interpretation of some masking studies, especially those involving integration, where either inhibition or summation may occur under different circumstances (e.g. Schiller, 1968).

The results of the psychophysical studies have provided strong evidence for the existence of sustained and transient

mechanisms in man. These presumably bear some relationship to the physiologically identified X and Y systems of animals. Some caution is necessary in identifying the two types of result, however, since it is possible to explain the results of many of the psychophysical studies in terms of a single mechanism which varies its response properties with changes in stimulation. This possibility is consistent with some physiological data. For example, de Monasterio (1978a) has demonstrated that the sustained or transient nature of the response of monkey retinal ganglion cells is often dependent upon the nature of the stimulus. It is likely that similar response changes occur in man. Even if the same cells do produce both sustained and transient responses, however, the following conclusions about the stimulus conditions evoking the two types of response remain valid. Although there is a considerable overlap, transient mechanisms respond best to low spatial and high temporal frequencies and sustained mechanisms to high spatial and low temporal frequencies. Transients respond to stimulus onset, offset and flicker, and sustained mechanisms to stationary or slowly moving stimuli. The latter produce a prolonged response to a pattern and may thus be responsible for visible persistence. This will be discussed in the next chapter.

The results of many of the studies cited in this chapter indicate that sustained mechanisms process pattern, whereas transient mechanisms process temporal information. These mechanisms are not independent, however, but interact in such a manner that the spatial properties of a stimulus affect the visual analysis of its temporal characteristics,

and vice versa (e.g. Kelly, 1972b). Many of the spatio-temporal properties of the visual system, including persistence, may consequently result from this interaction between transient and sustained mechanisms. In the following chapters of this thesis possible means by which sustained and transient mechanisms interact to influence persistence duration under various experimental conditions will be considered. Since, as is discussed in chapter 2, persistence may be a suprathreshold manifestation of temporal integration in the visual system, the contributions of sustained and transient mechanisms to phenomena such as temporal integration and flicker sensitivity will also be considered (chapter 3).

CHAPTER 2

VISIBLE PERSISTENCE AND ICONIC MEMORY

2.00 General Introduction

It has long been known that the visual sensation resulting from a brief pulse of light may last longer than the actual duration of the stimulus. After its offset, an internal representation or "copy" of the stimulus remains for a measurable period of time during which its strength appears to decay (e.g. Haber & Hershenson, 1973). The nature of this phenomenon of visible persistence is the subject of the present chapter, which reviews the literature on the topic, and concludes that there are at least two components to persistence, one retinal and the other cortical. It then proceeds to evaluate the literature on iconic storage and concludes that measures of iconic storage involve persistence, after-images and non-visual factors (e.g. Coltheart, 1980).

Boynton (1972) has described how D'Arcy in 1773 made the first attempt to quantify visible persistence by measuring the maximum time required to produce an apparent complete circle when a light was mounted on a rotating wheel. His estimate of persistence duration was 133 msec (Boynton, 1972). A number of different methods have obtained varying estimates since that time, generally ranging from about 100-300 msec. This variability in measures of persistence appears to be due, not only to different methods of measurement and experimental conditions, but also to differences in definitions and concepts of visible persistence.

A number of investigators have related visible persistence to the observation that subjects appear to briefly retain a decaying representation of a letter array stimulus after its termination (Averbach & Sperling, 1961; Coltheart, 1975; Sperling, 1960). A letter or letters can apparently still be "read" on presentation of a cue several hundred msec after the stimulus. This ability to "read" information after the offset of the original stimulus has been interpreted as evidence for the existence of an entity variously called "visual information store", "short term visual memory", or "iconic store" or icon (Neisser, 1967). From such a storage unit, information is thought to be transferred to more permanent memory (Sperling, 1967). The hypothesised transmission of visual information through an iconic store is part of the visual information processing approach (Haber & Hershenson, 1973).

Not all authors agree that it is necessary to postulate the existence of an iconic store, and as Eriksen and Schultz (1978) have noted, the concept creates a number of problems. They argue that the icon is "the persistence for short durations of the neurological activity in higher visual centres resulting from stimulation of the retina" (Eriksen & Schultz, 1978, p. 1). Alternatively, iconic memory may be a form of temporary non-visible attachment of physical information to a permanent internal lexicon (Coltheart, 1980), a process which is completely different to persistence. It is becoming clear that the terms "iconic storage" and "persistence" are not necessarily synonymous and it is considered desirable to clarify the usage of these terms. In this thesis "iconic store", "visual information store" and

"short-term visual memory" will be used to refer to the storage unit inferred from the results of partial-report and some backward masking experiments. The phenomenon investigated by more direct measures of response duration will be referred to as "visible persistence" (Coltheart, 1980) although the term may not have been used by the original investigators (e.g. Haber & Standing, 1969; Meyer, Lawson & Cohen, 1975).

Visible persistence will be defined as any continued visible response to a stimulus occurring subsequent to stimulus offset but which is phenomenally indistinguishable from that occurring while the stimulus is present. It is distinguished from an after-image in that the latter is a visible effect that continues after the perceived termination of the stimulus (Brown, 1965).

This discrimination between "visible persistence" and "iconic storage" is in line with several recent publications which have proposed modifications to the persistence terminology, especially that of Coltheart (1980), who similarly distinguishes between the two concepts. The phenomenon described by "persistence" in this thesis may also be equivalent to Type I Persistence (Hawkins & Shulman, 1979; Long, 1979b) or "phenomenal persistence" (Turvey, 1978). Iconic storage is probably identifiable with "Type II Persistence" (Hawkins & Shulman, 1979; Long, 1979b) or "informational persistence" (Turvey, 1978). The relationship between persistence and iconic storage will be discussed in more detail subsequently.

2.10 Visible persistence

Although there are a number of studies in which persistence has been investigated as a basic characteristic of the

visual system, it has more often been studied within an information processing context. The persisting image has been considered to be responsible for short-term visual storage. Consequently, many investigators seeking to study iconic storage have investigated persistence, and the latter's existence has been regarded as evidence for iconic storage (e.g. Coltheart, 1975). As these studies have investigated persistence in an information processing context, they have normally used either letters or forms such as circles, squares, or outline pictures as stimuli (Briggs & Kinsbourne, 1972; Haber & Standing, 1969, 1970).

Interest in the spatio-temporal properties of the visual system has resulted in the use of grating stimuli (e.g. Meyer & Maguire, 1977). Experiments using these types of stimuli will be considered under "persistence of form". Visible persistence may be measured by relatively direct methods such as those of Haber and Standing (1969, 1970) which estimate the total apparent duration of a stimulus. An alternative method (Eriksen & Collins, 1967, 1968) measures the time interval over which the information from two successive stimuli may be integrated. This method, which generally results in shorter estimates of persistence than more direct methods, will be called the integration method. It has also been referred to as the "successive field paradigm" (Sakitt & Long, 1978).

Investigators interested in persistence as such have generally used light flashes as stimuli in parametric studies investigating the effects of variables such as stimulus intensity and duration (Bowen, Pola & Matin, 1974; Efron, 1970a, b, c). Both direct (Bowen et al., 1974)

and integration methods (Di Lollo, 1977; Hogben & Di Lollo, 1974) have been employed.

The following sections review the literature on persistence using the classification outlined above. Persistence of form studies will be considered first and the results of studies using the different measurement techniques will be compared. Studies using light flashes as stimuli will then be described, followed by a section dealing with other phenomena which may be due to mechanisms similar to visible persistence.

Persistence of form studies and studies using light flashes are described separately since it is possible that slightly different mechanisms may be activated by the two types of stimuli. Light flashes are produced on dark (Efron, 1970a, c) or dimly illuminated backgrounds (Di Lollo, 1977; Di Lollo & Wilson, 1978) and consequently elicit responses to the change in luminance. Contoured stimuli are generally presented against backgrounds which are of similar luminance to the stimulus (e.g. Briggs & Kinsbourne, 1972; Haber & Standing, 1969; Meyer & Maguire, 1977). When luminance remains constant, the visual system responds, not to changes in luminance, but to changes in contrast. There is some evidence that the temporal response to contoured stimuli may be slightly different from that to pulsed spots of light (e.g. Breitmeyer & Ganz, 1977).

2.11 Persistence of form studies

2.111 The oscillating slit method

Haber and Nathanson (1968) measured persistence by varying the speed of a vertical slit oscillating in front of a

stationary form until an observer could just perceive the entire form simultaneously. The duration of visible persistence was estimated to be 240 msec (Haber & Hershenson, 1973). When the form, rather than the slit, was moved at the same rate, the percept was not identifiable. For a complete percept to occur, it was thus necessary for successive portions of the form to be "painted" across the retina, rather than to occur at the same retinal location (Haber & Nathanson, 1968).

2.112 Separation threshold measures

Haber and Standing (1969), and subsequently Meyer and colleagues (Meyer et al., 1975; Meyer, 1977) have used a method in which the stimulus was alternated repeatedly with a blank ISI of variable duration. It was assumed that, although flickering, the alternating stimulus would appear to be continuously present until the duration of the ISI exceeded the duration of the persistence of each cycle of the stimulus. The ISI at which the blank becomes just detectable is consequently a measure of the persistence of the stimulus. Haber and Standing (1969) obtained a mean estimate of persistence of 261.2 msec for a high luminance stimulus, and of 295.7 msec for a low luminance stimulus with this method. When the ISI was dark, persistence increased to 405 msec. Haber and Standing also presented alternate cycles of the stimulus to different eyes and concluded from their results that persistence occurs in the visual cortex. Long (1979a) and Coltheart (1980), have argued that dichoptic presentation does not necessarily indicate that an effect is cortical since all monocular

activity must feed into central binocular channels before a percept can occur. The experiment of Haber and Standing (1969), therefore, does not necessarily indicate that persistence is generated in the cortex.

Using the same method, Meyer and Maguire (1977) have demonstrated that the persistence of grating stimuli increases with increasing spatial frequency. Although their object was to investigate "grey-out elimination" rather than persistence, the similarity of the method used by Corfield, Frosdick and Campbell (1978) to that of Meyer and Maguire indicates that similar mechanisms were under investigation in the two studies. Corfield et al. (1978), using stimulus durations in the range 600-900 msec, demonstrated that "critical blank duration" (i.e. persistence) increases with increasing spatial frequency. It is interesting that considerable apparent persistence (100-350 msec) was observed at these long stimulus durations, since very little persistence has been observed with similar durations when alternative methods of measuring persistence have been employed (e.g. Haber & Standing, 1970). The question as to whether persistence occurs when long duration stimuli are used has recently been considered by Coltheart (1980) and will be discussed in more detail in subsequent sections of this chapter.

2.113 Onset-offset adjustment measures

Haber and Standing (1970) measured persistence by asking subjects to adjust the onset of a click to coincide with both the apparent onset and offset of a letter array stimulus. The difference between these provided a measure of the apparent duration of the stimulus. Persistence was

found to decrease with increasing stimulus duration up to about 200 msec, so that the apparent duration of the stimulus remained relatively constant over this range. For stimulus durations appreciably longer than 200 msec negligible persistence was observed. With dark pre- and post-exposure fields maximum persistence increased to about 400 msec, as compared with a value of about 175 msec for light pre- and post-exposure fields. This is similar to the increase in persistence observed with a dark ISI in the separation threshold method.

2.114 Reaction time measures

Briggs and Kinsbourne (1972), Erwin (1975) and Erwin and Hershenson (1974) have attempted to measure persistence by subtracting the reaction time to the onset of a stimulus from the reaction time to its offset. Estimates of persistence reported in each of these three papers are, however, considerably shorter than those obtained by other direct methods, being no more than 70-80 msec for 100 msec stimuli (Briggs & Kinsbourne, 1972). This discrepancy may indicate that subjects are responding on the basis of cues other than the apparent duration of the stimulus, possibly to transient responses occurring at the offset of the stimulus (Boynton, 1972). It has been shown that reaction time responses can be obtained under circumstances in which a probable transient response occurs, although the stimulus producing this is not detectable (Fehrer & Raab, 1962). A transient response occurring at the offset of a stimulus may consequently trigger a reaction time response, although the phenomenal persistence of the stimulus may continue.

Those studies which purport to be measuring persistence using reaction time procedures may thus instead be measuring the comparative latencies of on and off responses (see also Coltheart, 1980).

2.115 Integration of successive stimuli

The basic assumption underlying this method is that while a response to a stimulus continues to persist, it will integrate with a subsequently presented stimulus to form a composite percept. Increasing the ISI between the two stimuli will allow more time for the persisting response to the first stimulus to decay, resulting in a deterioration in the clarity of the composite and consequent decreased identification accuracy. The maximum ISI at which the composite can be identified at above chance level is thus a measure of persistence.

The best known experiments using this paradigm are those of Eriksen and Collins (1967, 1968). Two dot patterns which yielded a three letter nonsense syllable when superimposed were constructed. The syllable was not identifiable from either pattern alone. Subjects were required to identify the syllable when the two stimuli were presented successively. Identification accuracy declined markedly over ISIs of 25-75 msec, levelling out for ISIs greater than 100 msec. This decrease in performance with increasing ISI was considered to represent the decay curve of the persistence of the first stimulus. It was hypothesised that increasing the energy of the first stimulus by increasing its duration would result in a more intense trace producing improved identification accuracy. When the duration of either stimulus was increased

beyond 50 msec, however, identification accuracy was not greater than that expected from chance alone at an ISI of 20 msec (Eriksen & Collins, 1967). Overall, an apparent decrease in persistence was observed when the duration of either stimulus increased. A subsequent experiment (Eriksen & Collins, 1968), in which the luminance of the two stimuli was varied systematically, provided some support for the hypothesis that a more intense stimulus produces a stronger trace. Performance was better when a high luminance stimulus was followed by one of low luminance than when the order was reversed. There were, however, indications in the data that more is involved in the integration of successive stimuli than a decaying sensory trace. Eriksen and Collins (1967, 1968) considered that their data provided evidence for the existence of "discontinuity detectors" (possibly transient on- and off-responses: Phillips and Singer, 1974) which interfere with the integration of successive stimuli especially when these are of unequal luminance.

The integration method of measuring persistence duration employed by Eriksen and Collins (1967) produced an estimate of approximately 100 msec. This is considerably shorter than the persistence durations of up to 300 msec frequently obtained with more direct methods (excluding reaction time). It is proposed later in this chapter that the reason for this discrepancy between the results of the two methods is that they measure persistence at different levels of the visual system. Integration methods may only involve the summation of energy at peripheral levels, whereas the more direct methods may also include persistence occurring

within the visual cortex.

2.12 Persistence studies using light flashes

The following group of experiments differs from those considered above as the experimenters were directly interested in persistence as a perceptual phenomenon rather than as a means of providing information about iconic storage.

2.121 Onset-offset adjustment measures

Efron (1970a, b) investigated the duration of a percept compared with the physical duration of a stimulus. He used a homogeneous coloured field presented briefly on a dark background. The duration of the percept produced by this stimulus was measured by adjusting the onset of a field of a different colour to coincide with either the onset or offset of the first field. This method is similar to that of Haber and Standing (1970) and Sperling (1967). The second field was separated 6^{o} 16' horizontally from the stimulus and subjects were asked whether they saw a temporal gap or overlap between the two stimuli. With brief stimuli, Efron (1970a, b) found that the first stimulus appeared to be present for about 230 msec. This total apparent duration remained constant for all stimulus durations shorter than 130 msec. The difference between the apparent duration of the stimulus and its actual duration (i.e. persistence) consequently decreased linearly with a slope of -1.0 as a function of increasing stimulus duration. The relationship between persistence and stimulus duration could thus be expressed by: persistence (P) + stimulus duration (t) = a constant (D). This relationship was found to hold for all

stimulus durations less than about 130 msec. For long stimulus durations persistence remained constant as stimulus duration increased. Efron's data can thus be described as follows:

$P + t = D$ (minimum perceptual duration) $t < 130$ msec

$P = k$ $t > 130$ msec.

(k = constant)

It was not possible to obtain accurate estimates of the minimum perceptual duration because it could not be assumed that the perceptual onset delay of the comparison stimulus was equal to the perceptual offset delay of the test stimulus. The results of a further study (Efron, 1970c), however, indicated that under the conditions of this experiment the minimum perceptual duration was close to 130 msec. In contrast to the previous studies no persistence was observed at long stimulus durations. This study was performed in a similar manner to the other studies, except that a click was used as the comparison stimulus instead of a second field. Coltheart (1980) has noted that persistence is found to occur at long stimulus durations when the comparison stimulus is of the same sensory mode as the test stimulus but not when the two stimuli are of different sensory modalities.

Efron (1970c) also demonstrated that visible persistence decreased logarithmically with increasing luminance. These results are not consistent with the sensory trace hypothesis which predicts an increase in persistence with increasing energy (e.g. Eriksen & Collins, 1967, 1968).

Bowen et al. (1974) measured persistence by adjusting the onset of a probe flash situated to the left of the main

stimulus to coincide with either the onset or offset of the latter. Comparison and test stimuli were thus presented in the same sensory mode. Persistence durations ranging from 200-300 msec were obtained. Persistence was again found to decrease with both increasing flash intensity and stimulus duration, and considerable persistence was also observed at long stimulus durations.

It was found that the decline in persistence with increasing duration did not occur if equal energy stimuli were used. This result would imply either that the crucial variable affecting persistence duration is energy, or that the effects of duration and intensity are additive, so that an increase in duration just cancels the effect of a decrease in luminance (Coltheart, 1980). This finding has not been replicated, and conflicts with data obtained by Di Lollo and colleagues who have shown that persistence is inversely related to duration in an integration paradigm in which equal energy stimuli are always used (Di Lollo, 1977, 1980; Di Lollo & Wilson, 1978; Hogben & Di Lollo, 1974).

2.122 Integration measures

Di Lollo and colleagues have used a temporal integration technique to investigate persistence. To enable the location of a missing dot to be correctly identified, the visual system must integrate information presented over a period of time so that it appears to be simultaneously present. The paradigm required subjects to identify the location of a missing dot when 24 of a 5 x 5 matrix of dots were plotted on an oscilloscope screen (Hobgen & Di Lollo, 1974;

Di Lollo, 1977). The physical duration of each dot was very brief (50 μsec), and dots were presented sequentially, so that no two dots occurred together. Due to persistence, the apparent duration of each dot was much longer than this, so that all dots appeared to be present simultaneously at brief interdot intervals. Consequently, the location of the missing dot was easily identified. When the total plotting interval was greater than 120 msec, however, apparent simultaneity no longer occurred, and identification accuracy deteriorated. A similar result was obtained when the 24 dots were presented in two separate bursts (a procedure very similar to that of Eriksen and Collins, 1967). The duration of persistence as estimated by this method was consequently no greater than 120 msec.

Further studies using variations on this procedure have indicated that the physical duration of dots is a crucial variable determining time over which integration occurs. If one dot is presented for 100 msec, its location is frequently mistakenly identified as that of the missing one, indicating that it fails to integrate with the remaining dots (Di Lollo, 1977). Similarly, a burst of dots presented for this duration fails to integrate with another burst presented 10 msec subsequently (Di Lollo & Wilson, 1978). Di Lollo (1977, 1980) has argued that the neural response to a stimulus takes a finite length of time, about 120 msec, to complete. The response is considered to commence at the onset of a stimulus and to continue for 120 msec, or for the duration of the stimulus, whichever is the longer. Thus visible persistence, as measured by the interval over which two or more stimuli

integrate, is considered to be residual neural activity occurring after the offset of the stimuli. Persistence and stimulus duration are thus inversely related over stimulus durations less than 120 msec, confirming the relationship obtained by Efron (1970a, c).

Estimates of the duration of persistence obtained by Di Lollo's technique and by Eriksen and Collins (1967) are both approximately 100 msec. Similar values have been obtained using a variant of the integration method for measuring the span of phenomenal simultaneity (Allport, 1968, 1970; Efron & Lee, 1971). A rapidly moving object was illuminated stroboscopically and subjects were asked to count the number of images of the object apparently visible at the same time. This number, together with the frequency of stroboscopic illumination, provided an estimate of the duration of visible persistence. Efron and Lee (1971) obtained estimates of persistence ranging from 133-144 msec. In addition, the span of phenomenal simultaneity was found to be inversely related to the luminance of the stroboscope. Allport (1968, 1970) observed that this relationship (a power function with an exponent of -0.13 or -0.16) closely paralleled that occurring with the critical duration of temporal brightness summation. He therefore proposed that persistence and the critical duration reflect the same underlying process.

The above results indicate that estimates of persistence obtained using integration methods are quite consistent with each other and are generally shorter than those obtained using the more "direct" methods. There is, however, one

study which gives somewhat longer estimates.

Rohrbaugh and Eriksen (1975) showed that integration of brief exposures of matrices of illuminated squares to form horizontal or vertical gratings may occur over a time period greater than 224 msec. In this experiment, however, information regarding orientation may have been available from other sources as well as from the formation of a composite percept. Apparent motion may occur over a longer time than integration (Kahneman, 1967). It is possible that the direction of the apparent motion resulting from the successive presentation of adjacent squares may thus have provided adequate orientation information for intervals up to 224 msec.

The studies involving the measurement of the persistence of light spots and flashes have provided estimates of up to 300 msec using direct methods and of approximately 100 msec with integration methods. These are similar to the estimates obtained from the persistence of form studies with the same techniques. There is thus no indication that the persistence of contoured stimuli differs substantially from that of light flashes.

In the majority of the studies cited above the authors did not attempt to identify the location of the persistence effect within the visual system. It is probable that integration methods predominantly measure persistence at the peripheral level (the evidence for this will be discussed subsequently). There are a number of studies, however, which provide evidence that persistence may occur in the visual cortex, or at least that its duration may be modified by cortical processes. These will now be described.

2.13 Evidence for cortical involvement in persistence

2.131 Stereoscopic persistence

When disparate stimuli such as Julesz dot patterns are presented to each eye, stereodepth is perceived by normal subjects. This depth perception still occurs when the stimuli are presented to each eye successively rather than simultaneously. The monocular persistence of the response may account for this observation to some extent. The duration of the depth percept may, however, be much longer than the overlap of the monocular responses alone, indicating the existence of binocular stereoscopic persistence at the cortical level (Dodwell & Engel, 1963; Engel, 1970). Engel's results indicate that there are two distinct stages in the generation of a percept from brief presentations of binocularly disparate stimuli. The first stage is monocular and presumably peripheral, whereas the second stage occurs at the level of the interaction of monocular channels in the visual cortex.

The characteristics of these two stages may differ, as the work of Ross and Hogben (1974) indicates. Using a stochastic dot sterogram method these workers have investigated the extent to which delays between presentations of trains of random points to each eye affect ability to perceive depth. Subjects were able to detect and identify objects in depth for lags between comparable points up to 72 msec. Depth was not readily discernable for delays longer than this, suggesting that persistence of information for use in steropsis is limited to about 70 msec. This value was unaffected by stimulus luminance. Using the same trains of

random points, however, apparent simultaneity occurred for presentations over a 120 msec interval. This interval increased with decreasing illumination. It is thus apparent that different tasks using essentially the same stimuli measured different persistence characteristics. The two tasks involved are apparently estimating persistence at different levels of the visual system. Depth perception involves the integration of information at the level of the visual cortex, whereas apparent simultaneity is probably produced by integration of information at the peripheral level. It is quite possible that persistence at these different levels is characterised by different time constants and affected differently by variables such as luminance.

2.132 The effect of orientation-specific adaptation upon persistence

The work described above indicates that there are apparently two types of visible persistence, a monocular form, and a cortically located persistence which prolongs the percept of stereodepth. This research clearly indicates that persistence may result from cortical activity under some circumstances. Further work implicating cortical activity in persistence is that of Meyer et al. (1975) and Meyer (1977). In these experiments the separation threshold method was used to investigate the effect of orientation-specific adaptation upon the persistence of high contrast gratings. It was demonstrated that persistence decreased after adaptation to a stationary grating of the same orientation. No decrease was observed when the test grating was orthogonal to the adaptation grating.

This adaptation effect was shown to transfer interocularly. Although the studies were considered to support the notion that persistence is cortical, Coltheart (1980) has pointed out that this interpretation suffers from the same difficulties as interpretations of cortical activity based upon dichoptic presentation. He also considers that the decrease in persistence observed after adaptation is inconsistent with the known inverse relationship between persistence and stimulus intensity, since, contrary to the expectations of Meyer et al. (1975), persistence should increase with decreasing contrast. Coltheart suggests that Meyer's results may even indicate that persistence is a peripheral effect since reducing contrast at a central level by adaptation does not have the same effect as reducing the actual contrast of a stimulus is likely to have.

Recent results by Lovegrove, Bowling and Gannon (Note 1) may indicate that cortical processes are involved in persistence since this is affected by orientation. Obliquely oriented gratings produced longer persistence durations than vertical or horizontal ones. These results do not demonstrate that persistence is entirely a cortical phenomenon but they do indicate that orientation specific mechanisms in the visual cortex modify the duration of persistence whether generated peripherally or cortically.

In this review of the persistence literature a number of properties of visible persistence have been established. It is consistently observed that persistence declines with increasing illumination and also with increasing stimulus duration. These properties appear to be quite robust and can be observed when differing methods of estimating persistence are employed (e.g. Allport, 1968; Bowen et al., 1974; Efron,

1970a, b, c; Di Lollo, 1977, 1980; Haber & Standing, 1970). Different measurement techniques, however, produce widely differing estimates of the overall duration of persistence. As discussed previously, reaction time methods apparently measure on- and off-response latency rather than the phenomenal duration of a stimulus, resulting in brief estimates of persistence. Disregarding this method, considerable variation also occurs among the results of other methods of measurement. Integration techniques consistently yield estimates of 100-130 msec with no persistence at long durations but onset-offset- adjustment and separation threshold measures may yield persistence durations of up to 300 msec, and appreciable persistence may be obtained with long stimulus presentations. In addition, both peripheral and cortical types of persistence may occur. To account for these differences between the various results it is necessary to postulate that visible persistence may occur at more than one location in the visual system, and consequently, that it is comprised of more than one component. Before outlining a possible two-component theory of visible persistence, the results of studies in a number of related areas will be described. These possibly provide further information about the nature of persistence.

2.14 Perceptual phenomena related to persistence

There are several perceptual phenomena which result from interactions between the responses to two or more successively presented stimuli. Many of these interactions apparently occur because of the limited temporal resolution of the visual system. Backward and forward masking, meta-

contrast and scoboscopic motion will be considered.

2.141 Backward and forward masking

Masking occurs when presentation of one stimulus inhibits detection or identification of a target stimulus presented before, during or after it. Many studies of masking have been considered to relate to persistence or iconic storage and a number have been devised to investigate the properties of the latter. In this section, Type A backward and forward masking (Breitmeyer & Ganz, 1976) by homogeneous light and by contoured stimuli will be discussed. Type B masking will be considered under metacontrast.

When a brief flash of light is presented in close temporal proximity to an intense masking flash, its detection threshold is increased (Crawford, 1947; Sperling, 1965). This threshold elevation declines exponentially with time after the offset of the masking stimulus. This decline has been considered to be a measure of the persistence function of the masking stimulus (Ganz, 1975). The results of Sperling (1965) who used a very brief masking flash indicated that masking declined over a period of 200-300 msec, a figure which is consistent with other measures of the persistence of light flashes (e.g. Bowen et al., 1974). The duration of this type of masking increases with increasing flash intensity, however, a result which is not consistent with the inverse relationship between luminance and persistence obtained with direct measures of persistence (e.g. Efron, 1970c). This type of masking study, especially where changes in the adaptation state of the eye are pronounced (Crawford, 1947), may therefore

involve factors not necessarily related to persistence, such as inhibition by on- and off-responses, or after-images. Masking by light flashes does not occur dichoptically, indicating a probable retinal location of this effect (e.g. Boynton, 1961).

Light flashes which occur in close temporal proximity to a contoured stimulus (target) also produce masking. For example, the recognition accuracy of target letters followed by a light flash is decreased for SOAs up to 100 msec in duration (Eriksen & Lappin, 1964). A similar recognition function is obtained when the flash precedes the target (forward masking). This type of masking does not occur dichoptically (Schiller, 1965). Forward and backward masking by light have been explained in terms of the luminance summation-contrast reduction theory (Eriksen, 1966; Eriksen & Lappin, 1964; Thompson, 1966). It is proposed that the responses to mask and target integrate to form a composite percept in which the contrast of the target is reduced in proportion to the luminance added from the mask. The lower apparent contrast of the target consequently reduces the detectability of the letters. Luminance summation is thought to occur as a result of limited temporal resolution in the visual system. Since temporal integration occurs over time intervals of approximately 100 msec, two stimuli presented successively at SOAs shorter than this will appear to be simultaneously present.

Although additional factors may be involved (Kahneman, 1968), the luminance summation-contrast reduction theory of

masking by light has generally been accepted as an adequate explanation of this. The theory has been extended to account for backward and forward masking by contoured masks as well as by light flashes (Coltheart & Arthur, 1972; Eriksen & Eriksen, 1971; Kinsbourne & Warrington, 1962a, b). Integration between responses to the target and contoured mask is considered to yield a composite in which the target letters are obscured by the contours of the mask. An alternative hypothesis which specifically relates to backward masking is that the after-coming pattern interrupts target processing or erases it from iconic store (e.g. Haber & Standing, 1968; Liss, 1968). Advocates of this theory consider that an undegraded icon is formed but that this cannot be identified due to an interruption in the transfer of the information to short term memory.

The relationship between degree of backward masking, energy of the mask, and ISI is complex, but generally recognition accuracy improves with increasing ISI, asymptoting after approximately 100-150 msec. Interruption theorists consider this effect to indicate that the icon is terminated by the arrival of the mask, and that the longer the ISI, the more time is available for transfer of material to short-term memory. A delay in the transfer of material to STM introduced by delaying a cue indicating which letter in an array is to be identified increases the interval over which backward masking occurs (Scharf & Lefton, 1970; Spencer, 1969). This result is consistent with a hypothesis that backward masking interferes with the transfer of information to a more permanent store. Further evidence in favour of the interruption theory of backward masking is given below.

Haber and Standing (1968) and Liss (1968) have shown that letters followed by a mask were seen by subjects to be of high contrast. Their apparent duration was, however, too short for the letters to be identified. These authors argued that integration between mask and target would prevent the formation of any recognizable high contrast target and interpreted their findings in favour of the interruption hypothesis. Spencer (1969) has shown that backward masking of 12-letter targets by pattern occurs for longer SOAs than backward masking by a light flash, indicating that mechanisms in addition to integration prolong backward masking under these conditions. Spencer and Shuntich (1970) have also shown that backward masking of 12-letter displays occurs over a much longer time period than forward masking of the same display (which can only occur as a result of integration mechanisms). The same authors found that, for stimulus onset asynchronies (SOAs) in excess of 150 msec, the energy level of the mask had no effect on the degree of masking. Since the integration hypothesis predicts that a greater reduction in target identifiability should occur with increased mask energy (e.g. Turvey, 1973), mechanisms other than integration must have been operative at these SOAs. Thus at long SOAs, pattern masks are more effective than homogeneous light masks, only backward masking takes place, and mask energy does not influence masking. It thus appears that at these SOAs a mask acts by interrupting or inhibiting target processing, rather than by integrating with the target.

Haber and Standing (1970) and Sperling (1967) have

directly measured the apparent duration of a target followed by a mask. The results were interpreted in terms of the interruption hypothesis as the target was seen to terminate at the onset of the mask. Breitmeyer and Ganz (1976) and Neisser (1967), however, consider that it is likely that subjects in these experiments based their judgements on transient responses to mask onset rather than on the apparent duration of the target. The high temporal resolution judgements required in this task would be expected to be based on the activity of transient, rather than sustained channels. Breitmeyer and Ganz, (1976, p.31) comment that "Judgements based on transient channel activity cannot be used to estimate temporal processes in sustained channels".

Although integration and interruption were originally viewed as competitive hypotheses, it is now clear that both processes may take place, the predominating mechanism depending upon many factors including mask and target energy, SOA, type of mask, and mode of presentation (Michaels & Turvey, 1979; Scheerer, 1973; Spencer, 1969; Spencer & Shuntich, 1970; Turvey, 1973). A series of studies by Turvey (1973) and Michaels and Turvey (1979) have indicated that masking is a complex phenomenon which may occur as a result of a number of mechanisms operating at both peripheral and central levels of the visual system. Since these mechanisms may be similar to those responsible for visible persistence, they will be discussed in some detail.

Interference between two stimuli may take place in several ways. If the stimuli combine to form a single package of information through integration or summation, the details of the target will be obscured by the contours of

the mask. Kinsbourne and Warrington (1962a, b) and Turvey (1973) found that the critical ISI at which a contoured mask no longer affected a target stimulus was related to the target duration by the formula; ISI x target duration = a constant. When target energy rather than duration was manipulated, the relationship became: ISI x target energy = a constant (power law). This power law was normally found only with monoptic or binocular presentation, rarely being observed with dichoptic viewing (Michaels & Turvey, 1979). Turvey suggested that these results may be explained in terms of the lack of fine temporal resolution in the visual system, the best known example of which is Bloch's Law. It was further suggested that the reciprocity between luminance and duration observed in the power law may be another manifestation of the processes underlying Bloch's Law. This mechanism has been referred to as "integration through within-net time sharing" (Michaels & Turvey, 1979). The observation that forward masking obeys the same power law is further evidence that this law describes integrative processes. Under conditions where the power law operates, the comparative energy of the fields is a significant variable determining masking, with high mask intensities producing greater masking than lower mask intensities. All of these characteristics suggest that the power law is indicative of processes occurring at a peripheral level of the visual system.

Under certain experimental conditions, backward masking occurs both monoptically and dichoptically and the degree of masking depends less upon the relative energies of target and mask than upon the stimulus onset asynchrony

between target and mask. Dichoptic backward masking is described by the relationship: target duration + ISI = a constant (additive law), and is considered to occur as a result of processes in the central visual system (Turvey, 1973, 1978). A further characteristic of dichoptic backward masking is that the relationship between degree of masking and ISI is frequently non-monotonic, maximum masking occurring at ISIs of up to 80 msec (Michaels & Turvey, 1979; Turvey, 1978). This resembles the non-monotonic function observed in metacontrast masking, which also obeys the additive rule and occurs dichoptically (Breitmeyer & Ganz, 1976).

Michaels and Turvey (1979) consider that backward masking at the central level is due to three processes, which are referred to as "integration through common synthesis", "interchannel inhibition" and "replacement". Integration through common synthesis refers to an amalgamation of information from target and mask at a central level, and occurs at short SOAs. Interchannel inhibition refers to the inhibition of the activity of sustained mechanisms by transient responses as proposed by Breitmeyer and Ganz (1976). The third type of masking is thought to result from an attention shift from target to mask processing as proposed by Turvey (1973). These types of central backward masking probably account for the results of the previously described experiments where the interruption hypothesis of backward masking was discussed (e.g. Scheerer, 1973). All of these results taken together provide reasonable evidence that interactions between two stimuli take place at central levels of the visual system.

The work of Turvey (1973) and Michaels and Turvey (1979) shows that backward visual masking occurs at both peripheral and central levels of visual processing. At the peripheral level masking is due to the summation of the energies of target and mask. Temporal integration or summation may occur at the level of the retinal ganglion cells. It has been shown that the duration of the response of (sustained) retinal ganglion cells in the cat may exceed 100 msec (Cleland, Levick & Sanderson, 1973). In addition, the responses of cat retinal ganglion cells to brief light pulses summate at short ISIs (Levick & Zacks, 1970). These properties of retinal ganglion cells thus provide the basis of an explanation of the limited temporal resolution in the visual system and of monoptic masking phenomena.

2.142 Monoptic backward masking and its relationship to persistence.

Monoptic forward and backward masking by structure have been explained in terms of integrative processes due to the limited temporal resolution of the visual system (Breitmeyer & Ganz, 1976). Methods of studying persistence which rely on the integration of information from two successive presentations may be similarly explained (Di Lollo, 1977; Di Lollo & Wilson, 1978). It is possible that the two phenomena may result from the same or similar underlying processes, the main difference being in the requirements of the task. In the backward masking paradigm, the target stimulus contains all the information required for correct identification and the contours of the mask are such that the target contours are obscured when the two are simultaneously present.

Conversely, in the persistence paradigm, neither stimulus contains all the information necessary for a correct response to be made and it is only when the two are present simultaneously that accurate performance occurs. Consequently, as the interval between the two stimuli increases, performance improves in a masking experiment but declines in a persistence task, since the extent to which the two stimuli appear to be simultaneous decreases.

If persistence and monoptic backward masking result from similar processes, it should be possible to make inferences about persistence from backward masking studies. There is, however, a problem with this assumption. As discussed previously, persistence appears to be best described by the relationship: stimulus duration + ISI (persistence) = a constant (Di Lollo, 1977; Efron, 1973). Persistence measured by the integration method occurs over a specific SOA (approximately 120 msec) regardless of the duration of the first stimulus. In contrast to this, the relationship describing peripheral backward masking is: critical ISI x stimulus duration (or energy) = a constant (Turvey, 1973). Different processes may thus be responsible for persistence and backward masking, at least to some extent.

There is some evidence that there may be two types of integrative processes taking place under backward masking conditions (Kahneman, 1968). When target and mask energies are approximately equal, linear summation between temporally overlapping responses may occur, but when the mask energy exceeds that of the target to any extent, the powerful mask

on-response may inhibit the target response. Schiller (1968) has demonstrated these two masking processes in single cells in the lateral geniculate nucleus of the cat. Further evidence for these two mechanisms may be obtained from a reanalysis of Kinsbourne and Warrington's (1962a) data performed by Ganz (1975). This analysis showed that when mask energy was less than twice target energy, masking occurred only at short SOAs by a process that appeared to involve summation between target and mask. When mask energy was considerably greater than target energy, changes in mask energy had no further effect on the masking ISI, and the relationship: critical ISI x target duration = a constant was observed. This relationship may be characteristic of an inhibitory, rather than of a summation mechanism.

The fact that persistence and monoptic backward masking obey different laws may be tentatively explained on this basis. Most persistence studies have used conditions in which the energy levels of the two stimuli were similar (e.g. Di Lollo, 1977; Di Lollo & Wilson, 1978; Eriksen & Collins, 1967). Such conditions would be optimal for temporal summation to occur. In those cases where there has been a difference between the energies of the two stimuli, performance was below that observed with equal energy stimuli (Eriksen & Collins, 1968). This suggests that as the energy difference increases, summation is less favoured and inhibitory mechanisms become more pronounced. Persistence is normally measured under conditions where summation occurs, whereas backward masking by visual noise is more often observed when mask energy is high relative to target energy and the inhibitory mechanism consequently predominates.

2.143 The relationship between persistence and forward masking.

Breitmeyer and Ganz (1976) have proposed that peripheral or Type A forward and backward masking may both be due to the limited temporal resolution of the visual system. The similarity between forward and backward masking (Kinsbourne & Warrington, 1962a, b; Turvey, 1973) indicates that similar mechanisms are involved. Forward masking, however, occurs over longer ISIs than backward masking. In addition, the duration of forward masking increases with increasing mask intensity (Schiller, 1966; Turvey, 1973). A similar effect of mask intensity may be observed with homogeneous light flashes (Sperling, 1965).

These differences between forward and backward masking may indicate that, although the basic mechanisms underlying both types of masking are similar, additional factors may influence forward masking. One of these may be powerful on-effects (or off-effects) produced by the mask (Boynton, 1961). These apparently reduce the sensitivity of visual mechanisms to subsequent stimulation for a period of time dependent upon the strength of the response.

The observation that masking duration increases with increasing intensity is inconsistent with an integration interpretation of forward visual masking, since the duration of temporal integration decreases with increasing intensity (e.g. Roufs, 1972a). A further observation of the nature of forward masking is also inconsistent with this hypothesis. Turvey (1973) found that increasing the duration of a mask over an interval of 10 to 100 msec had no effect on the

masking ISI. The integration hypothesis would predict, however, that as mask duration increases, masking ISI should decrease, since the duration of the mask response would remain constant (Di Lollo, 1980). There should be no masking when the mask duration is longer than its integration time. A number of studies show, however, that forward masking occurs over considerable ISIs even with long mask durations (Breitmeyer, 1980; Kinsbourne & Warrington, 1962b; Turvey, 1973).

These results consequently indicate that an integration, and hence, persistence mechanism, is insufficient to explain forward masking by pattern. There may however, be some circumstances under which forward masking by integration does occur. Di Lollo (1980) has shown that when mask energy is similar to target energy across all stimulus durations, the predictions derived from the integration hypothesis were confirmed. That is, masking ISI decreased with increasing mask duration, with very little masking being observed for mask durations longer than about 120 msec. In addition, when mask and target were presented simultaneously (for 20 msec) no masking was observed if the same mask had been continuously present for 80 msec or more prior to the target onset. In this case, the duration of the mask was greater than its integration time and its response would not have continued after mask offset. The response to the 20 msec target stimulus, however, would have continued for a further 80-100 msec after mask offset. A pure target response would thus have occurred for this time period, resulting in a clear target percept. It was argued from these results that persistence decreases with increasing stimulus duration (Di Lollo, 1980).

Di Lollo's results are clearly discrepant with Turvey's (1973) demonstration that mask duration did not influence masking ISI. The important difference between the experiments appears to lie in the degree of energy similarity between mask and target. Di Lollo (1980) equated the energy levels of target and mask, while other investigators did not. As discussed in the section on backward masking, different processes may operate when target and mask energy are similar than then they are different. Summation may occur when target energies are similar and inhibitory mechanisms predominate when mask energy is greater than target energy. Inhibitory mechanisms may include the on- or off-effects referred to earlier. Di Lollo's results may thus reflect summation processes, whereas the results of the other authors cited may result from the postulated inhibition mechanisms. In Turvey's (1973) experiment mask energy was much greater than target energy, even at the briefest target duration. With increasing duration, any tendency for masking ISI to decrease would be counteracted by the increase in mask energy and its consequent apparent intensity, which would tend to produce more prolonged off-response inhibition. With long duration masks, interference in the detection of brief target stimuli would be due entirely to off-response inhibition, accounting for the appreciable masking observed at these durations.

The above discussion is relevant for the interpretation of the results of an experiment recently reported by Brietmeyer (1980), who attempted to measure persistence duration using a forward masking paradigm. The rationale behind

the experiment was that a persisting visual response to a mask should produce a threshold elevation of a subsequently presented target stimulus, as occurs when target and mask are presented simultaneously. The ISI over which masking occurred was thus taken to be a measure of persistence duration. Using this method, Breitmeyer obtained results consistent with the hypothesis that persistence is longer in the fovea than in the periphery. Breitmeyer, however, used a 100 msec mask stimulus and a variable duration (presumably short) target stimulus. Target and mask luminances were not given, but the observation that masking occurred with long ISIs at this mask duration indicated that mask energy was high relative to that of the target. Conditions suitable for inhibition thus prevailed. It is consequently unlikely that Breitmeyer's method in fact measured persistence. Breitmeyer's data itself tends to confirm this deduction, since there was no increase in masking ISI with increasing spatial frequency. This is contrary to the results of a number of other investigators who have used different persistence measures (e.g. Meyer & Maguire, 1978).

2.144 Dichoptic backward masking and persistence

Backward masking may occur as a result of central as well as peripheral processes. Central backward masking obeys the additive law, is largely independent of mask energy, and the relationship between severity of masking and SOA may be non-monotonic (Michaels & Turvey, 1979; Turvey, 1973). It is similar in these respects to metacontrast which also occurs dichoptically.

The observation that interactions occur at central levels of visual processing indicate that neural responses to stimuli may persist for some time at this level. This persisting neural activity is not necessarily the same as iconic storage (Coltheart, 1980). The responses of cortical sustained cells are presumably prolonged for a specific time period during which they may be subject to interference with subsequent input causing masking. The proposed mechanism for dichoptic backward pattern masking is similar to that for metacontrast and will be described in more detail in the following section.

2.145 Metacontrast

Metacontrast occurs when a target stimulus is followed by a mask, the contours of which are closely adjacent to but do not overlap the target. Very little masking is observed when the SOA is zero with the degree of masking increasing with increasing SOA. It peaks at SOAs of between 50 and 100 msec, the position of the peak being independent of the duration of the target (Kahneman, 1967). It is evident that integration cannot explain the masking effect, since the target would not be obscured in a target-mask composite. An interruption or inhibition model at the cortical level seems more appropriate since the effect occurs dichoptically.

Breitmeyer and Ganz (1976) have proposed that metacontrast can be explained in terms of differences in the properties of sustained and transient cells. Sustained cells produce persistent responses at both the peripheral and cortical level (Cleland et al., 1973; Ikeda & Wright, 1975a) while transients have brief responses with short latencies.

Transient cells have been shown to inhibit sustained cells in cats (Singer & Bedworth, 1973), and this inhibition apparently also occurs in humans (Breitmeyer, 1975b; 1978). The visual response to any stimulus is thought to include a brief, rapidly transmitted transient response, and a longer, slower sustained one. In the metacontrast paradigm the target is hypothesised to produce sustained cortical activity lasting 100 msec or longer. When the mask follows the target at SOAs between 50 and 100 msec, the initial transient response to the mask may reach the cortex during the sustained response and inhibit this. The identifiability of the target is consequently reduced. When the target - mask SOA is shorter than 50 msec or longer than 100 msec, the transient activity is less likely to inhibit the sustained response since it is transmitted to the visual cortex either before the commencement of the sustained activity, or after it is completed.

Both metacontrast and dichoptic backward masking may thus result from the inhibition of a persisting neural representation in the visual cortex. The fact that the SOA remains constant indicates that the trace is initiated at stimulus onset and persists for a specific length of time which is independent of the actual physical duration of the stimulus. Studies with metacontrast and dichoptic backward masking thus support the hypothesis that a central form of persistence exists, and indicate that the duration of this persistence may be independent of stimulus duration.

2.146 Stroboscopic motion

If two spatially separate stimuli are presented successively, the first stimulus appears to move toward the second.

This stroboscopic (or phi) movement occurs even if the two stimuli are presented to alternate eyes, indicating that the mechanism responsible be located centrally (Kahneman, 1967). As for metacontrast, the SOA between the two stimuli is the crucial variable determining quality of motion, this being optimum for SOAs of about 100 msec (Kahneman, 1967; Kahneman & Wolman, 1970). Kahneman and Wolman (1970) argue that persistence of vision is responsible for this phenomenon, with apparent motion resulting from a temporal overlap between the neural responses to the two stimuli. The degree of overlap between the two responses is important in determining the quality of perceived motion. If the two stimuli are presented concurrently or with brief SOAs, the temporal overlap is considerable and the two stimuli appear to be simultaneous. If the SOA is long, little or no overlap between the responses will occur and the stimuli will be seen as successive. At intermediate SOAs (80-220 msec) apparent motion is observed, this being optimal at 100 msec for stimuli ranging in duration from 40-100 msec (Kahneman & Wolman, 1970).

These results again provide evidence for a central form of persistence whose duration is apparently independent of the duration of the stimulus but which may be affected by other experimental variables. Optimum apparent motion has been shown to occur at longer SOAs when the stimulus contains high spatial frequency information than it does when the high frequency information is removed (von Grunau, 1978). This is consistent with data indicating that persistence increases with increasing spatial frequency (Meyer & Maguire, 1977). The results of the metacontrast and stroboscopic motion studies thus indicate that a stimulus

gives rise to persisting neural activity in the visual cortex. During the first 100 msec this activity may be affected by incoming stimuli in such a way as to cause either masking or apparent motion.

2.15 A Two-component theory of persistence

From the previous review of the persistence literature it is evident that the results of various studies are not always consistent, especially with regard to the duration and location of persistence. There is a considerable amount of evidence to indicate that persistence is to a large extent peripheral. Evidence for the existence of stereoscopic persistence, however, indicates that at least some forms of persistence are due to central processes. Masking studies also show that interactions may take place at both peripheral and central loci, indicating that persisting neural activity occurs at both levels. Integrative methods of persistence measurement normally produce estimates of persistence duration of approximately 100 msec, whereas other more direct methods frequently produce estimates of up to 300 msec. Some of these differences may be purely methodological (e.g. reaction time measures may be tapping on- and off-responses rather than persistence), but others appear to indicate that persistence is a complex phenomenon, possibly comprising components at more than one level of the visual system. The various experimental techniques may be measuring different persistence components or some combination of these. It is hypothesised that persistence consists of two major components, one of which is peripheral and the other central. Although the existence of central persistence may be detected when long duration stimuli are

employed, not all methods of persistence measurement involve this component.

Even when very similar methods of persistence measurement are employed, considerable differences between the results of some studies occur. Efron (1970a) obtained longer estimates of the duration of persistence using another light flash as a comparison stimulus than he did when an auditory signal was used (Efron, 1970c). The reason for this difference is not known, but generally it appears that when test and comparison stimuli are of the same sensory modality, persistence estimates are longer than when they are of different modalities. Persistence is also observed at long stimulus durations in the former case (Coltheart, 1980).

The separation threshold method has been used several times to measure the persistence of patterned stimuli (Haber & Standing, 1969; Meyer et al., 1975). This method yields longer persistence values than most other direct methods and also produces appreciable persistence when the duration of the stimulus is quite long (Corfield et al., 1978). It may therefore measure a longer persistence component than many other methods.

As the two hypothesized persistence components appear to have different characteristics, a summary of the major findings related to persistence follows.

1. Under photopic conditions direct measures of persistence duration average about 250-300 msec (Haber & Standing, 1969). Estimates of persistence duration using procedures in which information from successive presentations is inte-

grated over time are, however, not greater than 120 msec (Di Lollo, 1977; Eriksen & Collins, 1967).

2. Apparent simultaneity of successively presented stimuli only occurs if the interval over which stimuli are presented is less than 120 msec (Allport, 1968; Hogben & Di Lollo, 1974).

3. The duration of the stimulus is an important factor in determining the duration of persistence as measured by both direct (Efron, 1970c) and integration methods (Di Lollo & Wilson, 1978). Persistence declines linearly (slope approximately - 1.0) with increasing stimulus duration up to a "critical duration" of approximately 130 msec (Efron, 1970a, c). The interval over which two stimuli integrate similarly declines as the duration of the first stimulus increases up to about 120 msec (Di Lollo & Wilson, 1978).

4. The duration of persistence decreases with increasing luminance (Bowen et al., 1974; Haber & Standing, 1969).

5. The persistence duration of gratings increases with increasing spatial frequency (Meyer & Maguire, 1977). This occurs for long as well as short stimulus durations (Corfield et al., 1978).

6. Peripheral types of backward and forward masking have some similarity to the persistence measured by integration methods and extend over SOAs up to about 100 msec (Coltheart & Arthur, 1972; Eriksen, 1966; Turvey, 1973).

7. Adaptation experiments (Meyer et al., 1975; Meyer, 1977) and the dichoptic results of Haber and Standing (1969) have indicated that persistence is partially a cortical

phenomenon. The usefulness of these results in inferring a cortical location for persistence has, however, recently been questioned (Coltheart, 1980).

8. Studies of metacontrast, dichoptic backward pattern masking and stroboscopic motion all indicate that interactions apparently due to neural persistence occur at a central level of visual processing (Breitmeyer & Ganz, 1976; Kahneman, 1967; Michaels & Turvey, 1979).

9. Central forms of backward masking may extend to SOAs well beyond 100 msec (Spencer, 1969; Spencer & Shuntich, 1970). This may indicate that neural persistence may last longer at the central level than at the peripheral level.

10. The existence of the persistence of depth percepts clearly demonstrates that cortical persistence occurs (Dodwell & Engel, 1963; Engel, 1973).

2.151 Peripheral persistence (Component 1)

It is hypothesised that the first persistence component is identical to temporal integration within the peripheral visual system. Although integration may also occur at the central level (Michaels & Turvey, 1979), the results of monoptic forward and backward masking experiments indicate that summation of stimulus energy is predominantly peripheral (Turvey, 1973). Most experiments involving the integration of successive stimuli indicate that this takes place over SOAs no longer than 100-120 msec. The finding that stimulus duration and persistence are inversely related for stimulus durations up to about 130 msec (Efron, 1970a, 1973) is thus

consistent with the data from integration experiments. The limited temporal resolution of the visual system, of which Bloch's Law is an example, may account for these findings. Because the visual system integrates luminance over time, the response to a very brief stimulus will be prolonged over the integration time causing the stimulus to appear to be present for approximately 100 msec. Peripheral persistence may thus be considered to be the difference between the duration of this response and the duration of the stimulus. Since integration time is not likely to vary with increasing stimulus duration, the total duration of a response will remain about 100 msec as long as the stimulus duration is shorter than this. Persistence duration will thus decrease linearly with a slope of approximately -1.0 as stimulus duration increases, until this is equal to or greater than the integration time, as Efron (1970a, c) has observed.

Most estimates of persistence duration obtained by integration methods are consequently approximately 100 msec, since two stimuli will form an apparent composite only if the second stimulus is presented while the peripheral response to the first is still occurring.[1] Since the duration of this response is invariant with stimulus duration for durations less than 100 msec, the interval between stimuli over which integration occurs is expected to decrease with increasing stimulus duration (Di Lollo & Wilson, 1978).

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[1] Successive field paradigm experiments producing longer estimates (Rohrbaugh & Eriksen, 1975; Sakitt & Long, 1978, 1979a) may have been confounded by after-images or cues other than integration, for example, the direction of apparent motion.

The integration of suprathreshold stimuli over intervals of about 100 msec may be compared with temporal integration measurements at threshold. The time over which time-intensity reciprocity (Bloch's Law) occurs is approximately 100 msec (Boynton, 1972). This critical duration, or integration time, beyond which Bloch's Law no longer holds, may also describe temporal properties at supra-threshold intensities. Evidence for the existence of a supra-threshold version of Bloch's Law has been obtained by Ueno (1977b), who obtained reaction times to light flashes varying in duration and luminance. The critical duration was obtained at 6 luminance levels and found to increase substantially as luminance level decreased. This agrees with the results of threshold studies, although the length of the longest critical duration was quite short when compared with the results of some threshold determinations (e.g. Barlow, 1958). The critical duration increases with decreasing luminance and also increases with increasing spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978). The link between peripheral persistence and temporal integration is consequently strengthened by the observations that persistence similarly lengthens with decreasing luminance (Bowen et al., 1974) and increasing spatial frequency.

The duration of the peripheral component of persistence may thus be described by the following relationships:

$$P_p = C - t \qquad t < C$$

$$P_p = 0 \qquad t > C \text{ --------- (1)}$$

where

P_p = peripheral persistence

C = critical duration

t = stimulus duration

2.152 Central persistence (Component 2)

As outlined above, there is considerable evidence that persistence occurs at a central as well as at a peripheral location. It is apparent that this form of persistence is only identifiable with certain measurement techniques. Integration methods requiring information to be summed at a peripheral level do not yield persistence with long stimulus durations (e.g. Di Lollo, 1977). Similarly, some onset-offset adjustment methods may only tap the transient on- and off-responses of peripheral mechanisms (e.g. Efron, 1973). Under these circumstances, no persistence is observed when stimulus duration is longer than the integration time, since in this case the peripheral neural response is presumably the same duration as the stimulus.

When considerable persistence is observed at long stimulus durations, it must therefore be due to mechanisms other than temporal integration at a peripheral level and result from a second persistence component. This component is hypothesised to be cortically located. Persistence is only observed at long stimulus durations when direct methods are employed to estimate its duration. These include intra-modal onset-offset adjustment methods (Bowen et al., 1974; Efron, 1970a) and separation threshold measures (Corfield et al., 1978). Estimates of the duration of persistence at these stimulus durations range from 100-200 msec although this depends upon various stimulus parameters such as spatial frequency (e.g. Corfield et al., 1978). Assuming the visible persistence of brief stimuli to be the sum of peripheral and central components gives a total

persistence duration of 200-300 msec, which is consistent with empirical estimates (e.g. Bowen et al., 1974; Haber & Nathanson, 1968; Haber & Standing, 1969).

Although the duration of the first persistence component varies inversely with stimulus duration, this appears to have little effect on the duration of the second component. Efron (1970a) found that the duration of persistence did not vary with increasing stimulus duration beyond 130 msec. The duration of the hypothesised second persistence component did, however, decline slightly with increasing stimulus duration in Haber and Standing's (1970) study.

Eriksen and Schultz (1978) consider that neural activity in the visual cortex may be characterised by a similar lack of temporal resolution to that occurring in the periphery. There is evidence that perceptual tasks such as form perception, which involve later stages of visual processing, yield much longer critical durations than those involving peripheral stages (Kahneman, 1966; Kahneman & Norman, 1964). Central persistence may thus be a manifestation of prolonged temporal integration at a cortical level.

2.153 The relationship between peripheral and central persistence

At present the information available is not sufficient for the relationship between peripheral and central persistence to be established. As observed previously, the sum of the durations of the two components is approximately the same as total persistence duration. Consequently the relationship between the two persistence components may be

additive. The persistence data of Efron (1970a) and the stroboscopic motion data of Kahneman and Wolman (1970) also suggest that total persistence duration may be the sum of a variable summation component and a relatively constant second component.

Turvey (1973), however, shows that, as far as backward masking is concerned, an additive model is insufficient to explain his data. He proposes an alternative - the concurrent and contingent model of the peripheral-central relationship. In this model the processes are assumed to overlap in time to some degree but the activity of the central process is dependent upon receiving input from the peripheral one. Such a model may explain why optimal metacontrast, which apparently involves persistence at central levels, may occur at relatively brief SOAs.

Although a concurrent and contingent model may be more suitable than an additive one, it is possible that the relationship between the postulated peripheral and central persistence components may be approximately additive in some cases. Assuming this to be the case and that the duration of central persistence does not vary with stimulus duration, the following relationship between the persistence components may be obtained.

$$P = C - t + Pc \qquad t < C$$

$$P = Pc \qquad t > C \text{ -------- (2)}$$

where

P = total persistence duration

Pc = central persistence

It follows that apparent duration (D) of a stimulus is

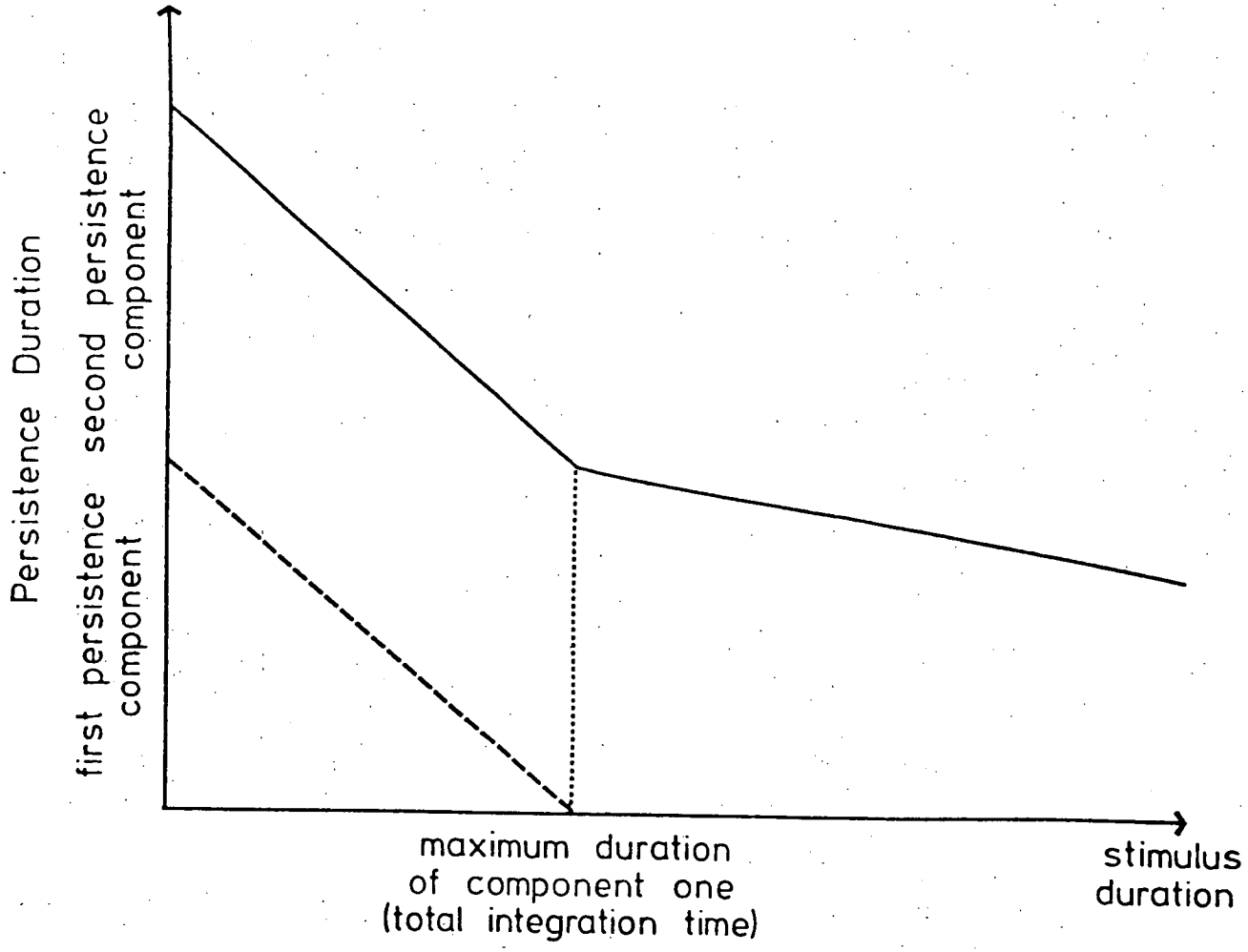

Figure 1. The hypothesised relationship between the first and second persistence components. The first component only occurs at stimulus durations shorter than the integration time, and decreases with increasing stimulus duration. The duration of the second component is relatively constant across stimulus durations, and adds to the duration of the first component.

$$D = P_p + t + Pc \qquad t < C$$

$$D = C + Pc \qquad t > C \text{ --------- (3)}$$

These hypothesised relationships are shown graphically in Figure 1.

Kahneman and Wolman (1970) have proposed a similar relationship between persistence, temporal integration time and stimulus duration without distinguishing between peripheral and central persistence components. Both Breitmeyer and Ganz (1976) and Eriksen and Schultz (1978) have identified two persistence components with characteristics similar to those outlined above. These two component theories are based on known or inferred properties of neurones involved in processing visual information. They differ from the two-component theory proposed by Erwin (1975) and Erwin and Hershenson (1974) in that their second component is considered to be influenced by cognitive factors, and is thus not a purely visual phenomenon.

In summary, it is concluded that visual persistence occurs as a result of neural activity at both the retinal and central levels of the visual system. The present chapter proposed that this prolonged neural activity is due to the nature of the responses of sustained neurons at retinal, geniculate and cortical sites and is not due to the activity of some specialised visual memory or iconic store. This raises the question of the relationship between persistence and iconic storage, which until recently (Coltheart, 1980) were thought to be identical. This question will be considered in the next section.

2.20 Iconic Storage

2.201 The partial report technique

As mentioned previously, the term "iconic store" will be used to refer to the storage unit which is inferred to exist from the results of studies using the partial report technique. An outline of this technique follows. Subjects are presented briefly with a letter array which contains enough elements to exceed the capacity of short-term memory. If asked to name all the elements, subjects are only able to recall an average of about 4.5 regardless of the number of items present (Averbach & Sperling, 1961). If, however, the stimulus is immediately followed by a cue to indicate which of the elements is to be recalled, performance is much better than that which would be expected from the whole-report result. Performance deteriorates with increasing delay between the stimulus and cue. The original experiments of this type were performed by Sperling (1960), who used a tone cue to indicate the line of a letter array to be recalled, and by Averbach and Coriell (1961) using a visual bar marker which pointed to an individual element of an array.

The accumulated results of many such experiments have provided strong evidence that visual information may be retained for several hundreds of milliseconds subsequent to the removal of the stimulus (Coltheart, 1975; Dick, 1974). The manner in which this information is retained is debatable, although it has been considered to be in the form of a visible trace (Averbach & Sperling, 1961) or after image (Sakitt, 1976)

It is not always agreed that the results of partial report experiments provide adequate evidence for the existence of iconic storage. Holding (1975) has argued that some results may be due to artifacts in the experimental design, including cue anticipation and output interference. These possible confounding factors, however, are not sufficient to explain all the data on iconic storage. In his reply to Holding, Coltheart (1975) has pointed out that the decline in performance with increasing cue delay cannot be explained by output interference. Neither can this explain the results of Averbach and Coriell (1961) who only required subjects to recall one element from an array. Since cue anticipation is also unlikely to be of major importance in well designed experiments, Holding's arguments are not convincing enough to cast doubt on the existence of some form of iconic storage.

Although the partial-report technique has been the most frequently used method of investigating the properties of iconic storage, a number of investigators have also used backward pattern masking. This was assumed to interrupt the processing of material in iconic store. It is becoming clear, however, that dichoptic backward masking may predominantly operate by inhibiting the persistence of cortical sustained cells, rather than by interfering with material in iconic storage.

2.21 The relationship between visible persistence and iconic storage

Iconic storage has been conceptualised as a fading neural "photograph" which retains information and which is separate

from the neural processes involved in transmission of the stimulus. Since a visible copy of the stimulus is presumed to be preserved more-or-less photographically, visible persistence has been postulated to be a possible mechanism for this (Averbach & Sperling, 1961). This hypothesis has some validity as stimulus features continue to be identifiable in a persisting visual image in the integration-type experiments of Eriksen and Collins (1967, 1968). Stimulus information should similarly persist for short delays in partial-report experiments. For example, integration between a letter array and a cue in the Averbach and Coriell (1961) experiment occurring at SOAs less than 100 msec would be expected to produce a composite from which the relevant information could be obtained. Persistence may thus be a mechanism underlying iconic storage under some circumstances. There are, however, a number of differences between the results of experiments on visible persistence and on iconic storage. These differences, which indicate that the two phenomena may be due to different processes, are oulined briefly below. They have been considered in detail by Coltheart (1980).

2.211 Differences between iconic storage and visible persistence

1. Duration

The period of time over which partial-report superiority occurs is frequently much longer than the duration of persistence (e.g. Sakitt, 1976; Sperling, 1960). This indicates that variables in addition to persistence influence iconic memory. These possibly include after-images (Hawkins &

Shulman, 1979) as well as non-visible factors (e.g. Coltheart, 1980; Sakitt & Appelman, 1978).

2. Effect of stimulus duration

A wide range of stimulus durations appear to have little effect on the duration of iconic storage (Coltheart, 1980; Dick, 1974; Sperling, 1960). This contrasts with the pronounced effect of duration upon visible persistence. An inverse relationship between the duration of persistence and duration of a stimulus has been reasonably well established (Efron, 1970a, c; Haber & Standing, 1970).

3. Effect of luminance

Using the partial report technique, increasing the luminance of a letter array has been shown either to have no effect upon icon duration (Scharf & Lefton, 1970), or possibly to increase it (Keele & Chase, 1967). The bulk of the literature relating persistence and luminance indicates that persistence decreases with increasing intensity (e.g. Bowen et al., 1974; Haber & Standing, 1970). Luminance consequently has opposite effects upon persistence and icon duration.

The evidence given above indicates that persistence and iconic store may be distinct phenomena. An alternative possibility is that different experimental techniques tap different aspects of the same basic phenomenon (Hawkins and Shulman, 1979).

2.22 The proposal of Hawkins and Shulman

Hawkins and Shulman (1979) suggested that the presentation of a stimulus gives rise to an exponentially decaying

sensory residual whose initial strength and duration are directly related to intensity. Direct measurements of persistence (Bowen et al., 1974; Efron, 1970c; Haber & Standing, 1970; Meyer et al., 1975) were thought to be based upon a response to the first detectable decrement in the strength of this residual. This detectable decrement is the minimum decline in the strength of the sensory residual which elicits a subject's awareness of stimulus offset. It was assumed to remain constant regardless of the initial strength of the residual. With a low intensity stimulus a longer time interval would be required to produce this decrement than with a high intensity stimulus. This accordingly explains the observed inverse relationship between intensity and persistence. Visible persistence which obeys this relationship has been defined by Hawkins and Shulman as "Type I persistence". In contrast to this, the partial-report technique and the click-indexing procedures used by Sakitt (1976) were considered to measure "persistence" at the stage of the decay curve where it declines to below threshold visibility. This gives rise to longer estimates of the duration of the residual and to a direct relationship between stimulus intensity and "persistence" duration. This second aspect of the same phenomenon, was called "Type II persistence" by Hawkins and Shulman. These authors considered that Type II persistence has similar characteristics to a positive after-image. It was thus implied that iconic storage is the result of a positive after-image.

Hawkins and Shulman's identification of Type II persistence and after-images was based on similarities between some results of Sakitt (1976) and known properties of after-images. Using a click-indexing procedure, high luminance levels, and dark-adapted subjects, Sakitt showed that the total duration of the visible after-effects of a stimulus increased with increasing intensity. Moreover, the after-effects appeared to be produced by the rod photoreceptors and were relatively long lasting (10 sec.). They thus possessed many of the characteristics of after-images, which are visible residuals observed after subjective stimulus offset, and therefore differ from visible persistence (Brown, 1965). The duration of after-images increases with luminance, with rods producing longer lasting after-images than cones (Alpern & Barr, 1962; Brown, 1965). They are normally produced by intense stimuli and may last for periods of several minutes. The luminance levels used by Sakitt were intense enough to produce weak after-images (Coltheart, 1980), and these were apparently responsible for iconic storage under the conditions of her experiments (see below).

2.23 The parallel components proposal of Long

Hawkins and Shulman (1979) made the first attempt to explain conflicting data on visible persistence and iconic storage. Their proposal that the same decaying sensory residual is responsible for both Type I and Type II persistence has, however, a number of difficulties. For example, it is generally assumed that visible persistence is principally a neural rather than photoreceptor phenomenon (although Coltheart, 1980, considers that persistence may

also involve the photoreceptors). It also apparently occurs at several levels of the visual system (e.g. Coltheart, 1980). In contrast, after-images are primarily due to changes at the receptor level and, by definition, only occur subsequent to observed stimulus offset (Brown, 1965). In addition, rods appear to be primarily responsible for Type II persistence whereas both rods and cones contribute to Type I persistence (Sakitt & Long, 1979a, b). It is thus unlikely that the same sensory residual is responsible for both types of persistence. The two types described by Hawkins & Shulman (1979) may represent two distinct mechanisms - visible persistence (Type I) and after-images (Type II).

Long (1979b) has proposed a modification of Hawkins and Shulman's model along these lines. His model is based on observations by Sakitt and Long (1979b) that subjects can distinguish target offset from the gradually fading after-image. Cone mechanisms appeared to be responsible for subjective offset, whereas rod mechanisms determined the total duration of the after-image. Both cone and rod "icons", however, showed a positive relationship to target luminance (Sakitt & Long, 1978, 1979a). Long consequently suggested that subjective offset is signalled by an off-response whose latency is inversely related to the luminance of the stimulus. The off-response was proposed to be produced by transient cells at the retinal ganglion level and higher, with the duration of Type I persistence consequently being determined by neural, rather than photoreceptor mechanisms. Type II persistence was assumed to be determined by the length of the rod after-image. He thus distinguished Type I

persistence, which is defined similarly to "visible persistence" as described in this chapter, from Type II persistence which may be considered to be a weak after-image (Coltheart, 1980). The suggestion that the duration of visible persistence may be determined by off-response latency has also been made by Coltheart (1980.

In the previous section of this chapter it was considered that the increase in temporal integration with decreased luminance may explain the inverse relationship between visible persistence and luminance. The mechanism by which luminance affects temporal integration, however, is not known. There is some evidence that integration time may be determined by the interval between on- and off-responses, this interval being relatively constant for brief stimuli (Efron, 1973; Serviere, Miceli & Galifret, 1977). Low luminance levels may increase this interval in some way, possibly by reducing the activity or increasing the latency of transient off-responses. Decreasing the strength of transient on- and off-responses by masking procedures does appear to increase integration time (Legge, 1978).

The evidence presented above suggests that iconic storage differs from persistence in several ways, and therefore that it does not result from the retention of information in a persisting neural image of the original stimulus. It has been suggested instead that it is due to retinal after-images (e.g. Long, 1979b). The remainder of this chapter continues to examine the nature of iconic storage with consideration being given to the possible relationship between iconic storage and after-images. This question has also been considered in detail by Coltheart (1980).

2.24 The relationship between iconic storage and after-images

The papers discussed in the previous section have drawn a distinction between visible persistence and weak after-images and have suggested that the latter are responsible for iconic storage. The work of Sakitt and Long (Sakitt, 1975, 1976; Sakitt & Long, 1978, 1979a, b) has focussed on this possible identification of iconic storage and after-images. There is some evidence that performance with the partial-report technique may be facilitated under conditions favouring the formation of after-images. For example, dark pre- and post-exposure fields, which increase the duration and strength of after-images (Brown, 1965) also increase the duration and accuracy of recall in a partial-report experiment (Averbach & Sperling, 1961). Sakitt (1975) has shown that a rod monochromat has similar iconic storage to that observed in normal subjects. Furthermore, stimuli which were initially invisible to this subject because of rod saturation became visible after she closed her eyes. This indicates that the rod photoreceptors are capable of retaining identifiable information. Consequently, rod after-images may be responsible to some extent for the ability to recall cued items from a stimulus array. The results of a number of studies indicate, however, that evidence for iconic memory may be obtained under conditions where rod after-images do not occur. Iconic memory consequently cannot be equated with iconic memory for the following reasons (see also Coltheart, 1980).

1. The luminances used by Sakitt were much higher than those used in many partial-report experiments. Many studies have provided clear evidence for iconic storage using stimuli which were too weak to saturate the rods and hence

generate a weak after-image.

2. Iconic memory is not wiped out when the stimulus is followed by a post-exposure field which is of a high enough intensity to saturate the rods (Averbach & Coriell, 1961). In this instance rod saturation would have eliminated the weak after-image.

3. When scotopically matched coloured letter arrays are used as stimuli, partial-report superiority is no different from that obtained using black letters on a white background (Adelson, 1978, 1979; Banks & Barber, 1977). In this case the colour difference between letters and background is invisible in the rods, and no rod after-image can be formed. In addition, Banks and Barber (1977) showed that colour information is available throughout iconic memory, indicating that colour coding mechanisms (cones) must be involved, at least initially.

The evidence given above indicates that neither visible persistence nor the weak after-image can fully account for iconic memory. An alternative conceptualization of iconic store than a decaying neural photograph must therefore be proposed. Coltheart (1980) considers that iconic memory may be due to the temporary attachment of physical information to a permanently existing entry in an internal lexicon. This attachment decays rapidly but some information may be stabilized by the operation of a mechanism called a "lexical monitor". This accounts for the decay of partial-report superiority with increasing cue delay. Coltheart considers that central backward masking may operate by preventing the lexical monitor from stabilizing information.

Although most backward pattern masking can be explained in terms of visible persistence as described above, Michaels and Turvey (1979) have demonstrated the existence of a form of central masking which appears to operate by reducing the time available for processing a target. They propose that the attention of a processing device is diverted from the representation of the first field to the second. The faster the first field can be processed the shorter the masking duration. Such a concept is not incompatible with Coltheart's proposal.

These suggestions of Coltheart (1980) and Michaels and Turvey (1979) are similar in that they consider iconic memory to include non-visible, probably higher-order cognitive processes in addition to visible ones. Iconic memory may thus not be the sensory store that it has been considered to be for so long but a combination of various visible and non-visible factors including persistence, after-images and higher-order phenomena.

2.30 Conclusions

It can be concluded from the arguments presented in this chapter that the presentation of a brief visual stimulus may give rise to a number of parallel processes. Stimuli shorter than about 120 msec produce a prolonged response, probably at the retinal ganglion cell level. This response lasts for the period of temporal integration and consequently persistence occurs for the time that the response duration outlasts that of the stimulus. An inverse relationship between peripheral persistence duration and stimulus duration is consequently observed. Integration

persistence does not occur when the stimulus is longer than its integration time. The peripheral response triggers sustained responses at the cortical level and these apparently persist for a relatively constant period over and above the duration of peripheral persistence. Peripheral and central persistence both constitute "visible persistence", which may be identified with Type I persistence of Hawkins and Shulman (1979) and Long (1979b).

In addition to the neural response, moderately intense stimuli produce weak after-images which are primarily due to saturation of the rod photoreceptors. These after-images increase in strength and duration with increased stimulus intensity and may be present for several seconds (Sakitt, 1976). They are visible, and appear to be responsible for some results attributed to persistence or iconic memory.

A third process which is contingent upon the visible neural activity is that responsible for iconic memory. This may be largely non-visible but presumably requires considerable visual processing before its establishment. It may thus occur subsequent to visible persistence. It is possible that the processes responsible for central persistence and iconic memory overlap to some extent, since both may be subject to interference by dichoptic backward masking.

It has been argued in this chapter that visible persistence, at least at the peripheral level, is one manifestation of the lack of infinite temporal resolution of the visual system. There are a number of temporal properties of vision which appear to have similar underlying mechanisms, and

which may therefore be related in some way to persistence. These will be described in the next chapter, which will also consider a sustained-transient mechanism as an explanation of many of these phenomena.

CHAPTER 3

SPATIO-TEMPORAL PROPERTIES OF VISION

It was proposed in the previous chapter that visible persistence results from neural processes occurring at two levels of the visual system. The first of these persistence components was hypothesised to be related to temporal integration at the peripheral level. Various stimulus parameters were shown to influence visible persistence in a similar manner to the way in which they affected other temporal properties of the visual system. The effects of these conditions upon various temporal factors are considered in this chapter.

Temporal properties of the visual system have been studied by measuring visual sensitivity to flicker, the detection threshold of two brief pulses of the same stimulus (two-flash threshold), and the duration of time-intensity reciprocity (Bloch's Law) at threshold. Each of these is affected by the luminance and spatial distribution of the stimulus and they consequently appear to result from similar neural processes to those producing persistence. The current chapter briefly considers these temporal studies and attempts to interpret the phenomena in terms of the sustained and transient mechanisms described in chapter 1.

3.10 Temporal factors in visual perception

3.11 Visual sensitivity to flicker

The visual system's response to flicker is studied by investigating the sensitivity to flicker of different temporal

frequencies under a number of conditions. The resulting relationship between sensitivity and temporal frequency is known as the temporal modulation transfer function (TMTF), de Lange curve, or temporal contrast sensitivity function. This function has a characteristic shape, with sensitivity increasing at low temporal frequencies, peaking, and then declining sharply at higher temporal frequencies. Although this shape is observed under a number of experimental conditions, the degree of low frequency attenuation depends upon various stimulus parameters. It is most prominent when the stimulus is a large edgeless field and decreases in prominence as field diameter decreases (Kelly, 1959, 1972a). This reduction in the low frequency attenuation is also observed if the flickering stimulus has a steady surround of the same mean luminance (Kelly, 1959; Roufs, 1972a). Similar changes in the shape of the curve at low temporal frequencies occur if the stimulus is a counter-phase flickering grating of medium to high spatial frequency (Kelly, 1971b, 1977; Robson, 1966). A large uniformly flickering field or a low spatial frequency grating (less than 1 c/deg.) produces a TMTF with a pronounced low frequency attenuation. With higher spatial frequencies this low frequency attenuation becomes less pronounced and is absent altogether when spatial frequencies greater than 4 c/deg. are employed (Robson, 1966). Measurements of contrast sensitivity at different temporal and spatial frequencies may be plotted as a three dimensional spatio-temporal surface (Kelly, 1972b, 1977). The shape of this surface indicates that the spatial and temporal aspects of vision are not independent of each other, with considerable

interaction between these occurring especially at low frequencies (Kelly, 1977).

The background illumination level also influences the shape of the TMTF in the low frequency region, the attenuation being increasingly reduced with decreased illumination (Kelly, 1971a, 1972a; Roufs, 1972a). At low luminance levels (less than about 0.3 cd/m^2) no low-frequency cut-off is observed.

3.12 The unit impulse response

Fourier transformation of the TMTF yields the unit-impulse response function of the visual system (Kelly, 1971a, b). This represents the predicted visual response to a very brief pulse of light. The shape of the unit-impulse response function is dependent upon that of the TMTF from which it is derived, and thus varies under different stimulus conditions. The TMTF with strong band pass characteristics obtained with a large uniformly flickering field or low frequency grating yields a unit impulse response function with a brief positive region followed by a pronounced negative lobe. In comparison, Fourier transformation of the TMTF obtained when the stimulus is a medium frequency (6 c/deg.) flickering grating yields a unit impulse response function with a more extensive positive lobe and no negative phase (Kelly, 1971b). A unit impulse response function similar to this is also derived from a TMTF obtained with low background luminance.

The impulse response of the visual system may also be studied by investigating the interaction between two brief presentations of a stimulus. Studies of this nature yield the summation function, which depicts the extent to which

the responses to the two stimuli summate over time. Unit impulse response functions derived from Fourier transformation of TMTFs, and summation functions obtained under similar experimental conditions closely resemble each other (Ganz, 1975), and both appear to describe a similar property of the visual system. Inverse Fourier transformation of the summation function can also be used to derive the TMTF (e.g. Rashbass, 1970).

3.13 The summation function

The summation function can be obtained by measuring the threshold detectability of two brief pulses separated by a variable ISI. At very short ISIs the two pulses are about twice as detectable as a single pulse, indicating almost complete summation. The degree to which the luminance of the two pulses is summed decreases as ISI increases, and at ISIs ranging from 50-70 msec, a phase of inhibitory interaction between the two pulses may be obtained. At still longer ISIs, the detectability of the two flashes is equal to that predicted from probability summation alone (Herrick, 1972; Ikeda, 1965; Roufs, 1973; Uetsuki & Ikeda, 1970). Ikeda (1965) and Rashbass (1970) also demonstrated that summation rather than inhibition occurred between the responses to a positive and a negative pulse if these were presented with ISIs of between 50-70 msec. This indicated that the visual system produces a bivalent response to a brief pulse of light. Using reaction time methods, Grossberg (1970) and Ueno (1977a) have shown that similar interactions occur between suprathreshold stimuli.

Changes in the shape of the summation function under different experimental conditions parallel changes in the unit impulse response function obtained from flicker frequency data under the same conditions. In particular, the inhibitory phase disappears when very small stimuli are employed (Meijer, van der Wildt & van den Brink, 1978), or when the stimulus pulses are high frequency gratings (Watson & Nachmias, 1977; Breitmeyer & Ganz, 1977). Meijer et al. (1978) have provided clear evidence that the presence of an inhibitory phase is dependent upon the size of the stimulus, showing that the negative lobe becomes more pronounced with increasing field diameter. No indication of a negative phase was obtained with pulse diameters of 11' or less under photopic conditions at a retinal eccentricity of 3.5^{o}.

The presence of the negative phase is also dependent upon background illumination and is absent under conditions of dark adaptation (Uetsuki & Ikeda, 1970; Ueno 1977a).

The time over which complete summation between the two responses occurs is also affected by the same variables as those affecting the shape of the function. Increasing summation is observed with decreasing field diameter, increasing spatial frequency and decreasing retinal illumination.

3.14 The duration of time - intensity reciprocity

For brief presentations, the threshold intensity of a flash of light is reciprocally related to its duration. Theshold intensity decreases with increasing duration so that their product remains constant. This relationship, known as Bloch's Law, holds for all flash durations shorter than a critical duration. For durations longer than this, perfect reciprocity no longer occurs.

The length of the critical duration is influenced by the same variables that affect flicker sensitivity and the impulse response. Under photopic conditions, it is shortened by increasing the pulse diameter (Barlow, 1958; Saunders, 1975) and by decreasing the spatial frequency of gratings (Breitmeyer & Ganz, 1977; Legge, 1978). Its duration is markedly increased by decreased illumination levels (Barlow, 1958; Sperling & Jolliffe, 1965). Roufs (1972a) has shown that it decreased monotonically with increasing luminance from 110 msec at about 0.03 cd/m^2 to 20 msec at 3.20 cd/m^2.

Using similar experimental conditons, a comparison of the critical duration of time-intensity reciprocity with the duration of complete summation in two-flash threshold measures reveals that a considerable discrepancy

exists between these two measures to temporal summation (e.g. Herrick, 1972; Roufs, 1973). Using the two-flash paradigm, complete temporal summation usually occurs only over very brief intervals (Boynton, 1972). Herrick (1972) found that temporal summation measured by the two-flash technique was about 40% shorter than the critical duration. Roufs (1973) found that the critical duration was approximately the same as the total duration of complete and partial summation of two flashes. He explained this observation by postulating that the eye only partially integrates luminance at two-flash intervals. greater than about 10 msec.

The data from single pulse experiments cannot be easily reconciled with those of flicker and two-flash experiments, although a number of models of the visual system have been proposed in an attempt to do this (e.g. Kelly & Savoie, 1978; Roufs, 1972b, 1974; Rashbass, 1970; Herrick, 1972).

Temporal integration has also been studied in single retinal ganglion cells of the cat (Levick & Zacks, 1970), and evidence for both time-intensity reciprocity and two-flash summation was obtained. A discrepancy between the two measures of temporal summation similar to that described above was observed, temporal resolution being more sharply defined in the two-flash situation than in the time-intensity

reciprocity measurement.

3.20 A sustained-transient model of spatio-temporal interactions in vision.

Many of the temporal properties described in the preceding sections may be explained in terms of sustained and transient mechanisms. The relative contributions of these two mechanisms may influence threshold sensitivity to flicker and to single and double pulse presentations under varying experimental conditions. The role of sustained and transient mechanisms in determining threshold sensitivity with varying field sizes and spatial frequencies will be considered first for each of the temporal properties under discussion. A possible means by which luminance level affects threshold sensitivity will be described subsequently.

3.21 The effects of field size and spatial frequency

3.211 Flicker sensitivity

It is probable that high frequency flicker predominantly activates transient mechanisms, and that stationary, or slowly flickering stimuli activate mainly sustained channels. Ikeda and Wright (1975a) and Movshon et al. (1978) have shown that transient (Y-like) cells in the cat visual cortex respond best to intermediate and high temporal frequencies, having a pronounced low temporal frequency reduction in sensitivity. Conversely, sustained (X-like) cells were most responsive to slowly flickering stimuli. Possible sustained and transient mechanisms with similar temporal properties to these have been demonstrated psychophysically in man. Kulikowski and Tolhurst (1973) have shown that separate contrast thresholds exist for pattern and flicker detection and have hypothesised

that these represent the activities of independent pattern and flicker detectors. The pattern detector preferred low temporal frequencies and thus resembled the sustained mechanism. The flicker detector was most sensitive to intermediate temporal frequencies, resembling the transient mechanism.

The spatio-temporal contrast sensitivity surface of Kelly (1972b, 1977) may thus be explained in terms of an interaction between sustained and transient mechanisms. Transient mechanisms are most sensitive to low spatial frequencies, and at these frequencies the temporal contrast sensitivity function thus resembles that of the flicker detector (Kulikowski & Tolhurst, 1973) showing low frequency attenuation. High spatial frequencies activate sustained mechanisms which decline monotonically in sensitivity with increasing temporal frequency. The low spatial frequency attenuation of the spatial contrast sensitivity function observed at low temporal frequencies (or with stationary gratings) may be explained similarly (Tolhurst, 1973).

Subjective observations recorded by Roufs (1972a, 1974) provide further evidence for a change-over from one mechanism to another with increasing temporal frequency. Roufs reported that the percept experienced when viewing a 1^{o} diameter uniform field flickering at low frequencies (less than 5-7 Hz) may be described as 'swell'. This appeared as a change in brightness occurring over the entire stimulus field. At higher temporal frequencies, however, the percept changed to one described as 'agitation' in which the brightness fluctuations were no longer homogeneous over the entire stimulus,with a 'swarming' effect being observed. He

proposed that the temporal contrast sensitivity of uniform field flicker resulted from the activity of two detectors. 'Swell' detectors were considered to be most active at low temporal frequencies, whereas 'agitation' detectors were thought to operate best at high temporal frequencies. The 'agitation' detectors appeared to act as band-pass filters. Changing the diameter of the flickering field was proposed to alter the relative sensitivities of the two sets of detectors. Although Roufs (1974) did not elaborate on correlations between his detectors and the properties of physiological mechanisms, he did point out that his concept of two detection systems is in agreement with physiological discoveries. The properties of his 'swell' and 'agitation' detectors appear to be similar to the properties of sustained and transient mechanisms respectively.

Differences in the properties of sustained and transient mechanisms may also explain the changes in the shape of the uniform field TMTF with decreasing stimulus diameter. Sustained cells have small receptive field centres with strong inhibitory surrounds and do not respond to large or diffuse light spots. Transient cells, however, are activated by spots of any size (Ikeda & Wright, 1972a). Large, edgeless fields would thus be expected to stimulate predominantly transient mechanisms whereas small fields may preferentially excite sustained mechanisms. The TMTF obtained with large fields (e.g. Kelly, 1959) may thus be a measure of the flicker sensitivity of transient mechanisms alone, showing their characteristic low frequency attenuation. Smaller fields may activate some sustained mechanisms, the proportion of these increasing as stimulus diameter decreases. Since

these are sensitive to low temporal frequencies, TMTFs obtained with smaller fields do not show the low frequency cut-off to the same extent as with large fields. The TMTF may thus be the envelope of the activities of both sustained and transient mechanisms, sustained ones predominating at low temporal frequencies and transients at high.

The presence of an illuminated surround also tends to remove the low frequency attenuation (Kelly, 1972a). This may be due to the adaptation and desensitization of the receptive field surrounds of both sustained and transient cells (Enroth-Cugell & Shapley, 1973; de Monasterio, 1978b). Desensitization of the surround mechanisms of sustained cells enables them to respond to larger than optimal stimuli, whereas desensitizing the surrounds of transient cells produces sustained-type behaviours (de Monsterio, 1978b). The presence of an illuminated surround may thus cause an increase in the proportion of sustained behaviour with a consequent increase in sensitivity to low temporal frequencies.

3.212 The summation function

Fourier transformation of the low frequency attenuated (transient-type) TMTF yields a unit impulse response function with a short period of temporal summation followed by a phase of inhibitory interaction. Similar shaped two-flash threshold summation functions may be obtained under the same experimental conditions as those yielding attenuated TMTFs; viz large uniform fields (Meijer et al., 1978; Rashbass, 1970) and low frequency gratings (Breitmeyer & Ganz, 1977; Watson & Nachmias, 1977). The summation function

characterized by the inhibitory lobe thus apparently represents the transient impulse response (Watson & Nachmias, 1977). High spatial frequency gratings and small uniform fields yield summation functions with no inhibitory lobe. These are similar in shape to the impulse response functions derived from the non-attenuated (sustained-type) TMTFs. The sustained impulse response is thus characterized by a relatively long period of temporal summation and no discrete inhibitory phase. The change in the shape of the summation function with increasing flash diameter observed by Meijer et al. (1978) is thus apparently due to a change in the predominant response mechanism from sustained to transient. This is similar to that occurring with decreased spatial frequency (Watson & Nachmias, 1977). Sustained mechanisms respond best to small fields, becoming less active as field diameter increases when a corresponding increase in transient activity occurs.

3.213 Time - intensity reciprocity

The increased duration of temporal integration with increased spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978) and with decreased uniform field diameter (Barlow, 1958; Saunders, 1975) may also be explained by the sustained-transient hypothesis. Transient mechanisms responding to brief presentations of large fields or low spatial frequencies with short response durations (Cleland et al., 1973; Watson & Nachmias, 1977) would be expected to produce short critical durations. Sustained mechanisms, on the other hand, appear to integrate intensity over longer time intervals since their response duration is considerably

longer than that of transient mechanisms. It is also possible that response duration varies within sustained channels, being longer for high spatial frequency channels than for those preferring intermediate spatial frequencies. The approximately linear relationship between spatial frequency and critical duration observed by Legge (1978) may thus be due both to a change-over from transient to sustained mechanisms, and to the longer response durations of sustained channels at higher spatial frequencies.

As mentioned previously, the nature of the relationship between the duration and threshold intensity of a single stimulus pulse is not readily predictable from the other temporal properties. Non-linearities in the temporal response occur at both the human psychophysical level (Kelly & Savoie, 1978) and at the single cortical cell level in cats (Tolhurst, Walker, Thompson & Dean, 1980).

The proportions of sustained and transient mechanisms activated by the different stimuli may provide a partial explanation of differences between the temporal summation properties of single flashes and those of two pulsed and flickering stimuli. The dominant mechanism responding to a pulsed grating of a particular spatial frequency at threshold may differ from that responding to a flickering grating of the same spatial frequency. Flicker activates transients to a greater extent than a single flash and transients may consequently determine thresholds at higher spatial frequencies for flickering stimuli than for single stimulus pulses. Comparison between Kulikowski and Tolhurst's (1973) threshold sensitivity data for flickering gratings and Legge's (1978) and Tolhurst's (1975a) data with pulsed gratings indicates that this may occur. For example, Kulikowski and Tolhurst's data indicate that transients determine

threshold for a flickering 3 c/deg. grating, whereas sustained mechanisms are responsible for threshold detection of a pulsed grating at a similar frequency (Legge, 1978; Tolhurst, 1975a).

It has been proposed that time-intensity reciprocity at threshold may result from prolonged responses of sustained retinal ganglion cells. A particular stimulus energy level would thus produce the same sustained response duration whether presented as a brief intense pulse, or as a longer less intense one, provided that its duration was less than the maximum duration of the channel's response. If two brief pulses of the same energy were presented within this period, however, transient off and on responses may also be triggered to the offset of the first pulse and onset of the second. These may have a mutual inhibitory effect (e.g. Phillips & Singer, 1974) and may also inhibit the sustained response to the two stimuli. This would cause the duration of temporal summation to be much shorter in the two-flash paradigm than in the single-flash paradigm, since it would be determined by the response durations of transient, rather than of sustained mechanisms.

Sustained mechanisms respond for the entire duration of a stimulus, whereas transient mechanisms only respond to stimulus onset and offset. Where transient mechanisms are responsible for threshold detection, increasing the duration of a stimulus beyond its critical duration should not further influence its detectability. If threshold is determined by sustained mechanisms, however, the longer the stimulus is present, the greater its probability of detection, since the sustained response may reach threshold at any time during the presence of the stimulus. This probability summation within

sustained mechanisms would result in some degree of partial integration occurring at stimulus durations longer than the critical duration. Where transient mechanisms determine threshold, no partial integration after the critical duration would be expected. Legge (1978) has shown that partial integration does not occur for spatial frequencies of 0.75 c/deg. or less, but does occur with frequencies greater than 1.5 c/deg. Harwerth et al. (1980) have demonstrated a similar result in monkeys. This indicates that transients determine detection thresholds at spatial frequencies less than about 1 c/deg. and that sustained mechanisms determine thresholds at higher spatial frequencies.

These results explain the presence of partial integration when very small uniform fields are employed (e.g. Barlow, 1958; Owne, 1972; Saunders, 1975) and its absence with large field diameters (Barlow, 1958; Rashbass, 1970).

3.22 The effect of background illumination

The low frequency attenuation of the TMTF and the inhibitory phase of the summation or unit impulse response function are absent at low levels of background illumination. The duration of time-intensity reciprocity also increases substantially with decreasing background illumination level (e.g. Roufs, 1972a). These changes are similar to those occurring with higher frequency gratings. That is, they are characteristic of the sustained mechanism. It may consequently be hypothesised that sustained activity predominates over transient activity at low levels of retinal illumination. Some recent physiological work supports this interpretation. It has been found that cat retinal ganglion

cells producing on- and off-responses at mesopic intensity levels give only a single sustained response at scotopic levels (Enroth-Cugell & Shapley, 1973; Yoon, 1972). In addition, Y cells clearly showing non-linear spatial summation were found to give sustained responses at low adaptation levels (Jakiela et al., 1976). It may be inferred from this that the changes in the shape of the TMTF and unit impulse response functions and the increased duration of temporal integration with decreasing adaptation level may be attributable to the increasingly 'sustained' behaviour of all cells under these conditions.

It has also been observed that the diameter of uniform fields has little effect on critical duration at low illumination levels (Barlow, 1958; Saunders, 1975). This may be explained by the changes in the receptive field properties of retinal ganglion cells that occur at low illumination levels. The inhibitory effect of the receptive field surround of (sustained) cells is reduced and the diameter of the excitatory centre increases (Barlow, Fitzhugh & Kuffler, 1957; Rodieck & Stone, 1965). The cell thus responds to larger stimuli or to lower spatial frequencies. It is likely that, under these conditions, sustained cells respond to stimuli of any diameter and that transient activity is reduced. Changes in field size thus would not change the predominant response mechanism and critical duration should remain relatively constant.

3.30 Temporal properties of suprathreshold stimuli

The material presented in the previous sections of this chapter has dealt with various temporal properties at threshold.

It was proposed in chapter 1 that both transient and sustained mechanisms respond to almost every stimulus but that the relative strength of their responses depends upon stimulus conditions. The stronger response is likely to attain threshold at lower contrast levels than the weaker response and a single mechanism may thus be responsible for the threshold detectability of a stimulus.

At suprathreshold contrasts, however, both mechanisms are likely to be above threshold and to contribute to the overall percept. Transient mechanisms may thus produce the percept of flicker in an alternating grating - blank sequence and sustained mechanisms may produce the percept of pattern. The pattern may appear to be continuously present because of the prolonged sustained response although clearly flickering due to transient mechanisms. Similarly, at suprathreshold contrasts, the offset of a pattern may be accompanied by a short-latency transient off-response followed some time later by the cessation of the sustained response. The inhibitory interaction between transient responses may also affect the percept produced by a sequence of stimuli, as in masking paradigms. In any consideration of temporal properties at suprathreshold contrast levels, the activities of both transient and sustained mechanisms must consequently be taken into account.

The majority of experiments aimed at identifying temporal properties of vision have used threshold sensitivity measures, although some experimentation at suprathreshold intensities and contrasts has been attempted using reaction time techniques (e.g. Grossberg, 1970; Ueno, 1977a, b). The

increment threshold technique (Boynton, 1961) has also been used to examine the temporal properties of supra-threshold stimuli, particular attention being paid to on- and off-responses (e.g. Battersby & Schuckman, 1970; Ikeda & Boynton, 1965). Masking studies also provide information about temporal behaviour at suprathreshold intensities and studies of visible persistence have also contributed to knowledge in this area.

In this chapter, the possible relationships between various temporal properties of the visual system have been discussed and an attempt has been made to relate these to sustained and transient mechanisms. The following experiments investigate the properties of one measure of temporal processing, visible persistence. It is attempted to relate this to temporal integration at threshold and also to consider it in terms of sustained and transient mechanisms as discussed in this chapter. As was described in chapter 2, visible persistence shows a considerable resemblance to the critical duration of time x intensity reciprocity at threshold. The aim of this thesis is to clarify the possible relationship between persistence and temporal integration. The subsequent chapters of this thesis describe experiments designed for this purpose.

CHAPTER 4

THE EFFECTS OF SPATIAL FREQUENCY AND CONTRAST UPON VISIBLE PERSISTENCE

4.00 General introduction

In chapter 3 the effects of spatial frequency upon various temporal aspects of the visual system were described. The duration of time-intensity reciprocity at threshold increases with increasing spatial frequency, as does the duration of the summation phase of the unit impulse response function. It was hypothesised in chapter 2 that visible persistence and temporal integration result from similar neural mechanisms. This hypothesis consequently predicts that the duration of visible persistence increases as a function of spatial frequency in a similar manner to the observed increase critical duration with spatial frequency.

Meyer and Maguire (1977) have shown that persistence does in fact increase with increasing spatial frequency. They used 50 msec presentations of high contrast square wave gratings and the separation threshold method of measurement. A similar result has been demonstrated with young children using sinusoidal gratings (Lovegrove & Heddle, in press).

Meyer et al. (1975) and Meyer (1977), have used adaptation procedures to investigate persistence. They hypothesised that adaptation to a grating of a specific orientation would result in a decrease in the persistence of a test grating of the same orientation due to the reduced apparent contrast of this grating (Blakemore, Muncey &

Ridley, 1973). A decrease in the persistence of square wave gratings was subsequently observed after adaptation to gratings of the same orientation. This reduction in persistence was not obtained when adaptation and test gratings differed by 90^{o}. Although their experiments demonstrated that adaptation results in reduced persistence, they did not provide any direct evidence that the contrast of the stimulus has any effect on persistence. It is possible that contrast has no effect, or even the opposite effect (Coltheart, 1980), and that these adaptation results may have occurred as a result of a mechanism other than the reduction in apparent contrast.

The following experiments were consequently performed to test the hypothesis that low contrast gratings have shorter persistence durations than higher contrast stimuli, and to investigate further the relationship between persistence and spatial frequency. The higher harmonics contained in the high contrast square-wave gratings used by Meyer and Maguire (1977) may have influenced persistence. Since the simplest stimulus analysed by the visual system appears to a sinusoidal grating (Campbell & Robson, 1968), this wave-form was used in the present experiments unless otherwise indicated. The contrast range of the sinusoidal stimuli was kept relatively low to prevent distortion of the wave-form. It was hypothesised that a similar increase in persistence with spatial frequency to that obtained by Meyer and Maguire (1977) would occur with sinusoidal stimuli of relatively low contrast.

Method (Experiments 1, 2 and 3):

Apparatus. Stimuli were presented by means of a Scientific Prototype 3 channel tachistoscope. The stimuli were photographs of sinusoidal gratings varying in contrast and spatial frequency. The space-average luminance of all gratings and of the blank with which they alternated was kept constant at 9 cd/m^2.

Subjects. These were volunteers predominantly recruited from under-graduate psychology classes and were unfamiliar with the hypotheses. All had normal or corrected-to-normal vision.

Procedure. Persistence was measured by a method similar to that of Meyer et al. (1975). The stimulus presentation was viewed binocularly. Each grating stimulus was presented for 50 msec and was alternated with a variable blank ISI for 10 cycles. The duration of the ISI was altered in 10 msec steps, except at very long ISI's (350 msec or more) when 20 msec steps were employed. Subjects were requested to report whether a distinct blank interval appeared between each grating cycle of the presentation. They were asked to report detection of the blank only if the grating appeared to fade completely between each cycle. They were instructed to ignore the obvious flicker of the cycling stimulus. A random staircase method was employed to obtain each subject's threshold for detection of the blank interval, the ISI being increased or decreased according to the subject's response on the previous trial. After each threshold reversal the ISI was either increased or decreased by 10 msec according to a previously randomised sequence. The initial ISI duration for each block of trials was chosen so that it was

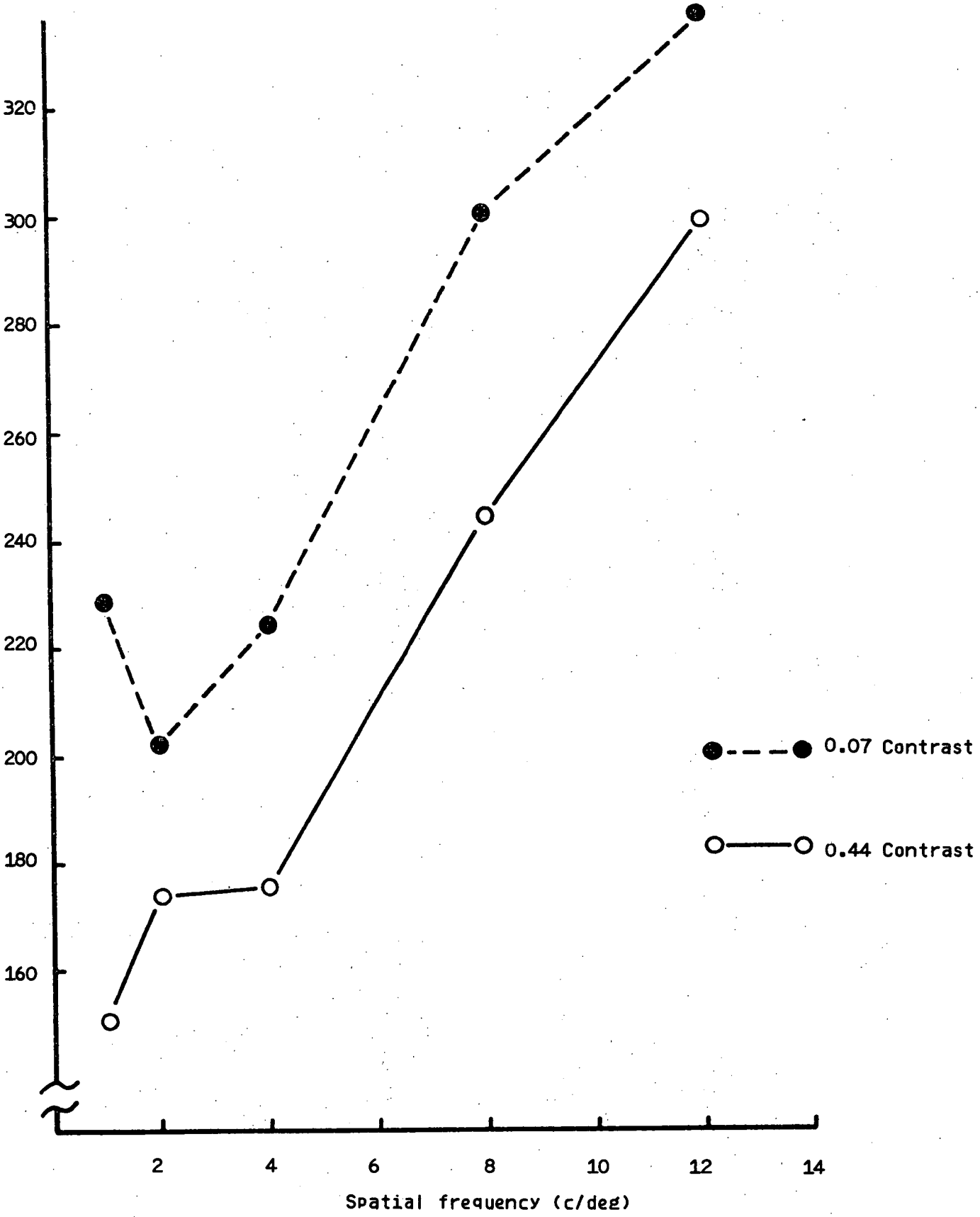

Figure 2. Mean persistence durations of two contrast levels of a sinusoidal grating as a function of spatial frequency of the grating.

either considerably above or below each subject's approximate detection threshold as determined during practice. Each block of trials consisted of six threshold reversals. The mean of these six threshold reversals for each stimulus was taken to be its persistence measurement. Data for each subject were obtained in a single experimental session which comprised an initial block of practice trials followed by the experimental trials.

4.10 Experiment 1

This experiment was designed to extend the results of Meyer and Maguire (1977) but with sinusoidal gratings and two levels of contrast. Repeated measures were taken over both factors. The spatial frequencies of the stimuli were 1, 2, 4, 8, and 12 c/deg and the Michelson contrast levels were 0.44 and 0.07. A circular field subtending 5 degrees of visual angle was used. Ten subjects participated and the order of presentation of the stimuli was counter-balanced according to a 10 x 10 Latin square.

Results

Mean persistence, in msecs, is shown in Figure 2 as a function of spatial frequency at both contrast levels. Persistence increased linearly with spatial frequency. A considerable difference between the overall means of the high and low contrast data was obtained with the persistence of the low contrast stimuli being longer than that of the high contrast stimuli. The analysis of variance showed that this difference between the contrast levels was significant ($F(1,9) = 6.6$, $p < 0.05$). There was no significant interaction between contrast and spatial frequency ($F(4,34) = 2.1$, $p > 0.05$) but the main effect of

spatial frequency was highly significant ($F(4,36) = 22.4$ $p < 0.001$). Comparisons between the means using Duncan's new multiple range test indicated that at both contrast levels the 12 and 8 c/deg gratings produced significantly longer persistence ($p < 0.01$) than the 1, 2, and 4 c/deg gratings which did not differ significantly from each other. In addition the persistence of the 12 c/deg grating was significantly longer ($p < 0.01$) than that of the 8 c/deg stimulus at the high contrast level. The difference between the overall means of the two contrast levels was 45 msec, and linear regression coefficients for the low and high contrast data were 11.9 and 13.2 respectively.

Discussion

The results of this experiment are in agreement with the findings of Meyer and Maguire (1977) that persistence increases with spatial frequency. A substantial increase in persistence with increasing spatial frequency was obtained for both low (0.07) and high contrast (0.44) sinusoidal gratings. There was, however, some difference between the two experiments in mean persistence at each spatial frequency. Mean persistence increased from approximately 300 msec at 0.9 c/deg. to 500 msec at 15 c/deg. in the Meyer and Maguire (1977) experiment, while for the high contrast condition in the current experiment it increased from 150 to 300 msec over a similar range of spatial frequencies (1 to 12 c/deg). This difference may be due to the differences between the luminance profiles employed in the two experiments although other factors such as

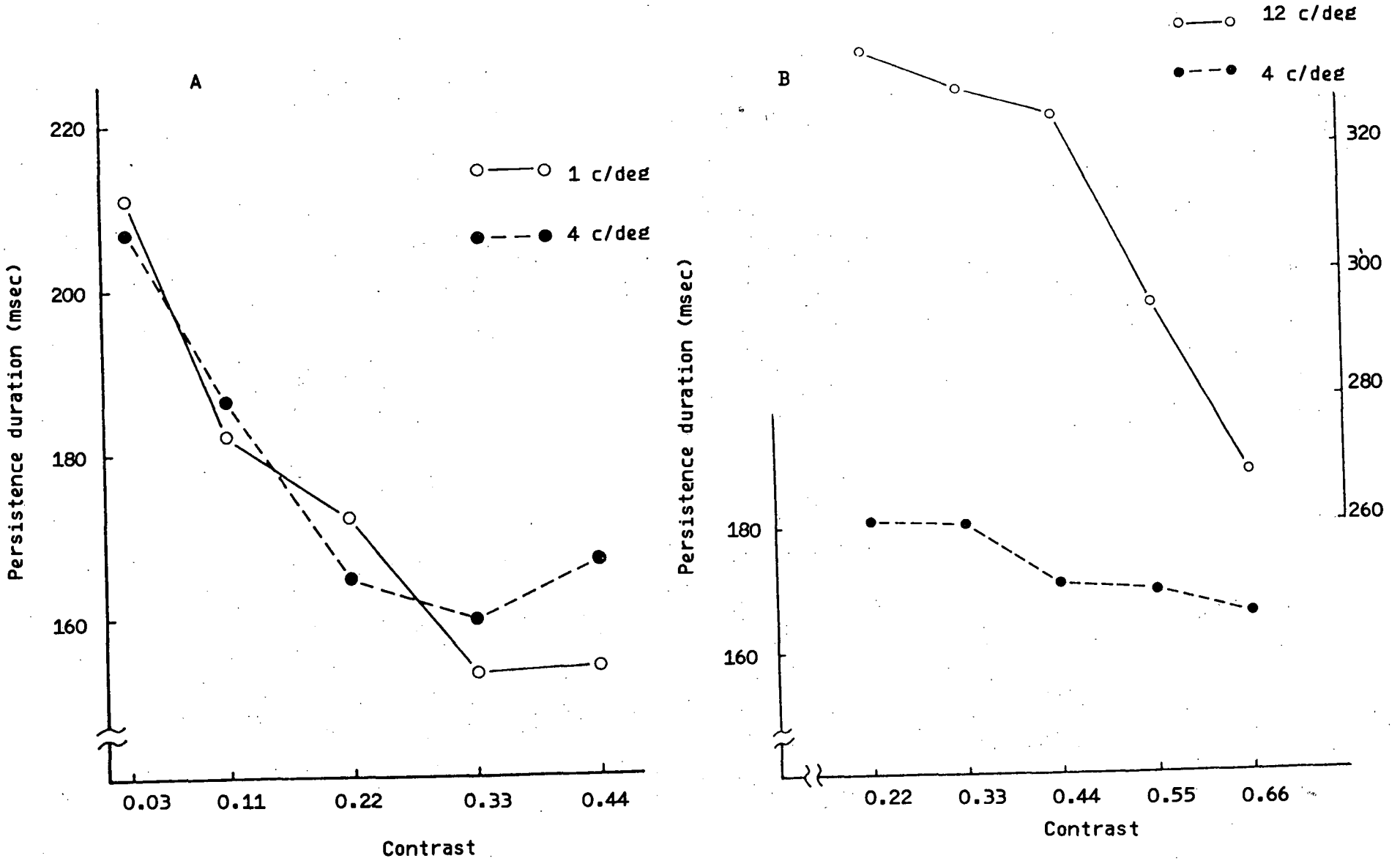

Figure 3. Mean persistence duration as a function of grating contrast; (A) 1 and 4 c/deg gratings (B) 4 and 12 c/deg gratings.

field size or individual differences could be important. Individual subjects varied from each other by as much as 200-300 msec in judgements of ISI duration at each spatial frequency in the present experiment. This apparently occurred as a result of different criteria employed by different subjects.

The finding that the persistence of low contrast gratings was longer rather than shorter than that of high contrast stimuli was contrary to the expected result. To obtain further information about the relationship between contrast and persistence, the effect of a range of contrasts upon persistence was examined. Experiment 2 reports the results of these investigations.

4.20 Experiment 2

This comprised two similar experiments, in both of which five contrast levels were used at each of two spatial frequencies. In the first experiment (2a) the contrast levels were 0.03, 0.11, 0.22, 0.33 and 0.44 at 1 and 4 c/deg. A 5^{o} diameter field was used. In the second experiment (2b), with spatial frequencies of 4 and 12 c/deg, contrast varied in steps of 0.11 units from 0.22 to 0.66. These higher contrast levels were necessary in this experiment since the alternating 12 c/deg grating was not readily visible to many subjects at contrasts lower than 0.22. The field diameter was 2^{o}. Ten subjects participated in each experiment.

Results

The mean persistence durations are shown in Figure 3 (a and b) as a function of contrast for both experiments

2a and 2b. The data for each spatial frequency are plotted separately. In general, a tendency for persistence to decrease with increasing contrast was observed for all spatial frequencies, although at lower spatial frequencies (1 and 4 c/deg) there was little effect of contrast upon persistence at levels above 0.22.

The analysis of variance of the data from experiment 2a gave a significant contrast effect ($F(4,36) = 11.9$, $p < 0.001$). Neither the spatial frequency main effect ($F(1,36) = 0.44$, $p > 0.05$) nor the spatial frequency x contrast interaction ($F(4,36) = 0.65$, $p > 0.05$) was significant. The Duncan's test revealed that the persistence of the 0.03 contrast grating was significantly longer ($p < 0.01$) than that of all the other contrast levels at both 1 and 4 c/deg. The 0.11 contrast was also significantly longer ($p < 0.01$) than that of the 0.33 and 0.44 contrast levels at 1 c/deg, and than that of the 0.33 contrast level at 4 c/deg. There were no significant differences between the persistences of the 0.22, 0.33 and 0.44 contrast levels. The effect of contrast upon persistence was thus most pronounced at low contrast levels.

The analysis of variance of the data from experiment 2b gave significant spatial frequency ($F(1,36) = 46.3$, $p < 0.01$) and contrast ($F(4,36) = 8.6$, $p < 0.001$) effects. A significant spatial frequency x contrast interaction was also obtained ($F(4,36) = 3.3$, $p < 0.05$). The Duncan's test revealed no significant differences in persistence between any of the contrast levels of the 4 c/deg grating. At 12 c/deg, the 0.66 contrast level produced significantly

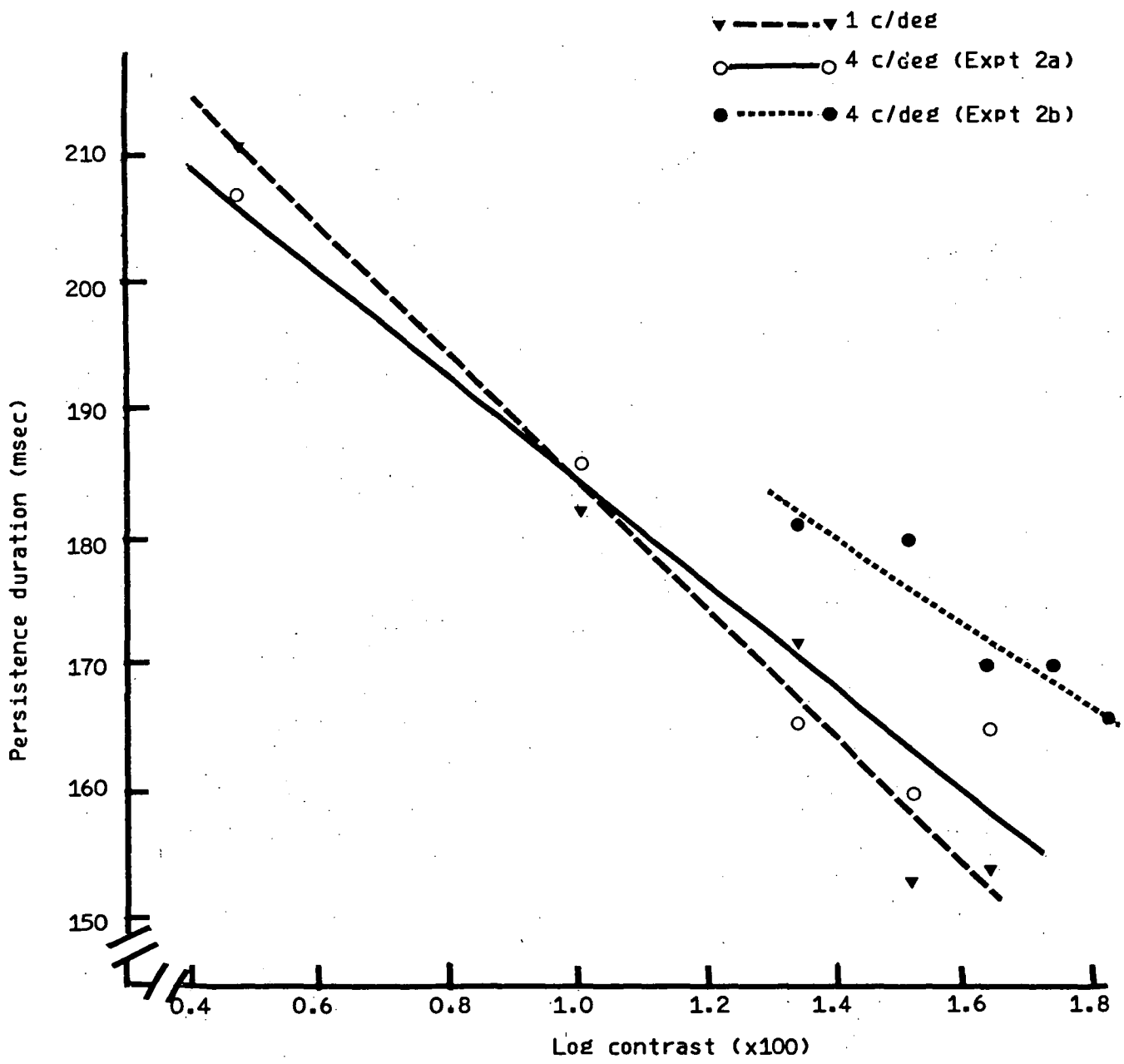

Figure 4. Mean persistence durations of 1 and 4 c/deg gratings replotted as a function of log contrast.

less persistence ($p < 0.01$) than the 0.44, 0.33 and 0.22 contrast levels which did not differ significantly from each other. The persistence of the 0.55 contrast level was, however, significantly shorter ($p < 0.01$) than that of the 0.22 contrast level.

The persistence data for the 1 and 4 c/deg stimuli from the two experiments were also plotted against log contrast as shown in Figure 4. This figure indicates that the relationship between persistence and log contrast is linear for these spatial frequencies. The linear regression coefficients were -51.32 for the 1 c/deg data, -41.65 for the 4 c/deg data from experiment 2a and -33.38 for the 4 c/deg data from experiment 2b.

Discussion

The results of these experiments indicate that persistence is elevated at low contrasts for each of the spatial frequencies investigated. At low spatial frequencies (1 and 4 c/deg) the relationship between persistence and log contrast was linear and the relationships for both frequencies had similar slopes. For the 12 c/deg grating, however, this relationship between persistence and log contrast was quite non-linear, differing considerably from that of the other two spatial frequencies in that the decline in persistence accelerated with increasing contrast.

This difference between the contrast x persistence relationships for low and high frequency stimuli may result from the difficulty some subjects experienced in perceiving the 12 c/deg stimulus, especially at medium contrast levels. The small, non-significant effect of contrast at these

contrast levels may be due to experimental artifacts.

The accelerated decline in the persistence of the 12 c/deg grating at higher contrast levels may partly result from a reduction in the apparent contrast of the 12 c/deg stimulus observed under the conditions of the experiment. Any perceived integration between the long blank ISI and the grating would reduce the apparent contrast of the grating considerably. It is possible that the apparent contrast of even the highest contrast 12 c/deg grating may have been low enough during alternation to be similar to that of the low contrast 1 and 4 c/deg stimuli. It is also possible that the relative contributions of sustained and transient mechanisms to persistence may account for the differences in the shapes of the contrast x persistence relationship between spatial frequencies (see general discussion).

4.30 Experiment 3

Sinusoidal gratings of high spatial frequency may have a lower apparent contrast than gratings of intermediate spatial frequency (e.g. Kulikowski, 1976). The preceding experiments have also shown that low contrast gratings produce longer persistence durations than high contrast stimuli. It is thus possible that the reduction in the apparent contrast of high spatial frequency gratings may account for their increased persistence duration as observed in Experiment 1. This possibility was investigated in the following experiment. Eight to ten photographs covering a range of contrasts of 2, 4 and 8 c/deg gratings were prepared. Subjects were asked to match the contrast of these with a 0.44 contrast 16 c/deg grating, so that a set

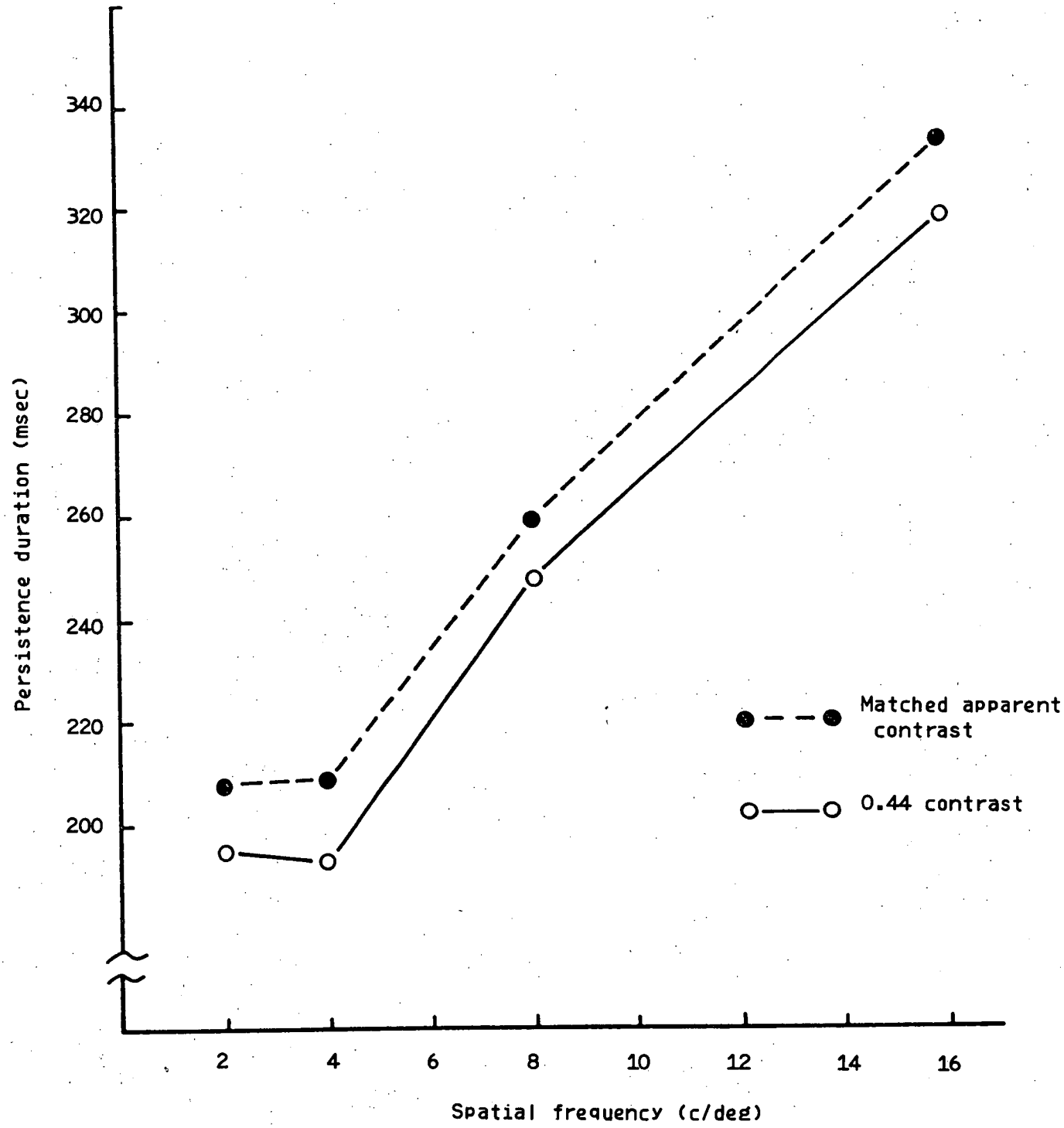

Figure 5. Mean persistence of gratings matched in apparent contrast and physical contrast as a function of spatial frequency.

of gratings matched in apparent contrast for each individual could be obtained. The 16 c/deg grating was presented to each subject through an off-centre 2^{o} diameter occluder in one field of the tachistoscope. The stimulus to be compared with the 16 c/deg grating was placed in a second tachistoscope field and the luminance of this field adjusted so that the two stimuli were matched in space-average luminance. An off-centre 2^{o} diameter occluder was similarly placed in the second field so the two stimuli appeared to the subject to be spatially adjacent when the two fields were switched on simultaneously. Each contrast was presented successively for each spatial frequency, until the subject chose the one most similar in apparent contrast to the 16 c/deg grating. The persistence of this set of 2, 4, 8 and 16 c/deg gratings matched for apparent contrast was then compared with that of 2, 4, 8 and 16 c/deg gratings of 0.44 contrast. The same 16 c/deg grating was used for each. The experiment was thus a 2 (matched apparent contrast and matched physical contrast) x 4 (spatial frequency) design, with repeated measures on both factors. Eight subjects participated. A 2^{o} diameter field was used.

Results and Discussion

The graph of persistence by spatial frequency for both contrast conditions is shown in Figure 5. The persistence of both the matched apparent contrast and 0.44 contrast conditions increased considerably with spatial frequency. The analysis of variance gave a highly significant spatial frequency effect ($F(3,21) = 20.2$, $p < 0.001$). A significant contrast effect was also obtained ($F(1,21) = 8.57$, $p < 0.05$), but there was no interaction between contrast and spatial frequency

($F(3,21) = 0.02$, $p > 0.05$).

The results obtained with the 0.44 contrast gratings replicate those obtained at the same contrast level in Experiment 1. In addition, the effect of spatial frequency on the persistence of gratings matched in apparent contrast was comparable to that obtained with the 0.44 contrast grating. This indicates that the increase in persistence with spatial frequency cannot be due to the reduced apparent contrast of high frequency gratings. A spatial frequency x contrast interaction was expected since the difference in actual contrast between the two contrast conditions would have been greatest at 2 and 4 c/deg, decreasing to zero at 16 c/deg. The lack of any interaction was probably due to the fact that the apparent contrast matching was conducted under steady viewing conditions where only slight spatial frequency related differences in contrast were obtained (e.g. Georgeson & Sullivan, 1975; Kulikowski, 1976). The contrast matching may therefore not have been adequate under the experimental conditions. Although the overall effect of contrast was significant, the persistence of each of the matched contrast 2, 4 and 8 c/deg gratings was consequently only slightly greater than that of the corresponding 0.44 contrast grating. Random variation in the persistence data for the 16 c/deg rating also resulted in an apparent difference between contrast levels at this spatial frequency, although the same stimulus has been used for each condition.

4.40 Experiment 4

The present results indicate that reducing the contrast of a stimulus is likely to increase persistence rather than to decrease it. It may therefore be necessary to postulate

that a mechanism other than contrast reduction is responsible for the adaptation results of Meyer et al. (1975). The experimental conditions used by Meyer et al. (1975) were, however, somewhat different from those employed in Experiments 1 and 2. They used high contrast (0.97) square wave gratings, whereas low to medium contrast sinusoidal gratings were employed in the present experiments. In addition, they used a 3^{o} by 5.5^{o} field size, luminance during testing was 1.42 ft-L (4.9 cd/m^2), and the spatial frequency of their test stimulus was 6.5 c/deg. These differences between the two groups of experiments may enable their explanation to be valid under their experimental conditions. It is, for example, possible that contrast has a non-monotonic effect on persistence. In this case, contrast reduction at the high contrast levels employed by Meyer et al. (1975) may result in decreased persistence duration.

This experiment was therefore carried out using experimental conditions as similar as possible to those used by Meyer et al. (1975). The stimulus was a 6.5 c/deg square-wave grating with a contrast as close to 1.0 as could be obtained. The two lower contrast levels also employed (0.8 and 0.6) were chosen so as to be similar to the apparent contrast expected to result from adaptation to a 1.0 contrast grating (Blakemore et al., 1973).

Method

The transilluminated square-wave grating of 1.0 nominal contrast was prepared by attaching narrow strips of black tape to cellophane. The space-average luminance of this stimulus was 4.9 cd/m^2. The grating was viewed binocularly from a distance of 150 cm to give it a spatial frequency

of 6.5 c/deg and a field size of 3^{o} by 5.5^{o}. The contrast of this grating was reduced to 0.8 by the superposition of a grey field (luminance 1 cd/m^2) from a second field of the tachistoscope. The luminance of the grating was reduced to 3.9 cd/m^2, to maintain the stimulus luminance at 4.9 cd/m^2. The 0.6 contrast stimulus was obtained similarly. Persistence was measured, as for experiments 1 - 3, by alternating the combined stimulus of grating and grey field with the blank ISI.

The method of limits was used to determine the threshold for detection of the blank interval (Meyer et al., 1975). Four threshold measurements were made in each block of trials. Two blocks of trials, presented in a counterbalanced order, were given for each contrast level. Eight subjects participated in the experiment. All were experienced observers and the majority had participated previously in one or more of experiments 1 - 3. A practice block of trials was given to each subject prior to commencement of the experimental blocks.

Results and Discussion

Mean persistence, averaged over the 8 subjects, was 285.3, 287.8 and 292.0 msec for the 1.0, 0.8 and 0.6 contrast levels respectively. The slight increase in persistence with decreasing contrast was not significant ($F(2,14) = 0.72$, $p > 0.05$).

This experiment thus shows that decreasing contrast does not result in decreased persistence under experimental conditions similar to those used by Meyer et al. (1975). In fact, a slight increase in persistence at lower contrasts

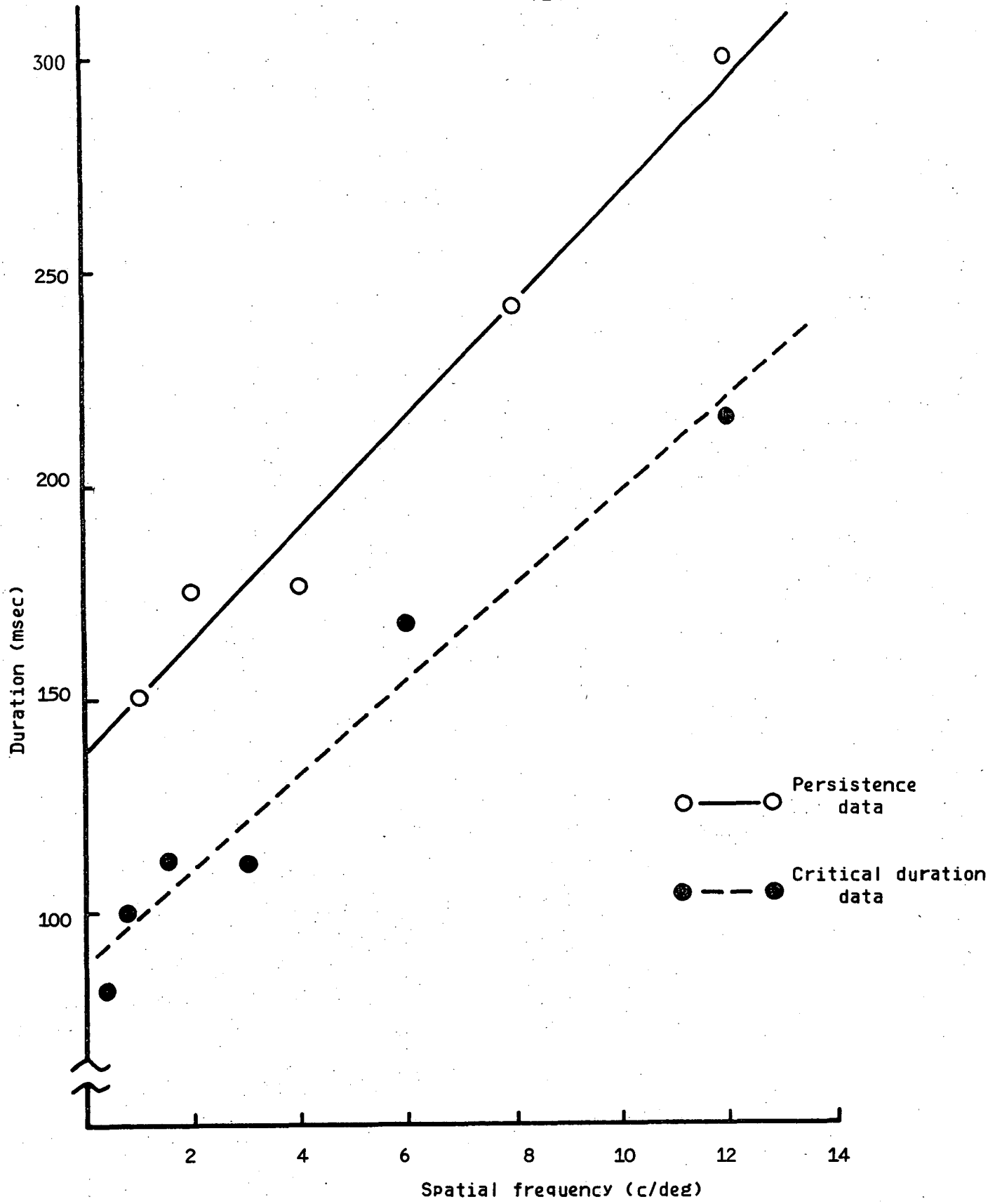

Figure 6. A comparison between the effects of spatial frequency upon persistence (data from Experiment 1) and upon critical duration (data from Legge, 1978).

was observed. The reduction in persistence as a result of orientation-specific adaptation (Meyer et al., 1975; Meyer, 1977) thus appears to occur as a result of a mechanism other than contrast reduction. This will be considered further in the general discussion.

General Discussion

The main findings of the above experiments were that visual persistence increases with increasing spatial frequency, and that it decreases with increasing contrast.

The increase in persistence with spatial frequency is similar to observations that both critical duration (Breitmeyer & Ganz, 1977; Legge, 1978) and duration of temporal summation (Watson & Nachmias, 1977) are dependent upon spatial frequency. The similarity between the effect of spatial frequency upon visual persistence and critical duration can be seen from a comparison of Legge's (1978) critical duration data with the high contrast persistence data from Experiment 1 (Figure 6). Both responses increase linearly with spatial frequency and the straight lines fitted to the data have similar slopes (regression coefficients were 13.2 for the persistence data, and 11.1 for the critical duration data). The persistence values were considerably longer than the critical duration data, as is generally the case in such comparisons (Ganz, 1975).

It has been hypothesised that the dependence of both critical duration and the summation function upon spatial frequency are due to the different responsiveness of transient and sustained cells to varying spatial frequencies (Breit-

meyer & Ganz, 1977; Watson & Nachmias, 1977). The finding that the persistence x spatial frequency relationship is linear may be evidence for a gradual change from transient to sustained activity with increasing spatial frequency. This hypothesis requires a considerable degree of overlap in the spatial frequency specificity of sustained and transient cells. There is some evidence of this in the data of Legge (1978), Tolhurst (1975a, b) and Watson and Nachmias (1977). Ikeda and Wright (1975a) also discovered a considerable degree of overlap in the peak spatial frequency sensitivity of cortical transient and sustained neurones in the cat.

It is also possible, however, that a spatial frequency dependent increase in the duration of sustained responses alone may occur (Breitmeyer & Ganz, 1976). It was proposed in chapter 2 that persistence at all spatial frequencies may be due primarily to the prolonged responses of sustained cells. Under these circumstances, the activity of transient responses at the offset of a stimulus may have an inhibitory effect on the sustained response (Breitmeyer, 1975b; Singer & Bedworth, 1973) reducing persistence. Since transients are predominantly responsive to low spatial frequencies, powerful inhibition of the sustained response following stimulus offset would greatly reduce persistence at these spatial frequencies. At high spatial frequencies the effect of transient off-responses on sustained activity would be minimal. A combination of long duration sustained responses and low transient activity may thus together account for the long persistences observed at high spatial frequencies. There is some evidence in the work of Eriksen and Collins (1967)

for such a reduction in persistence as a result of off-responses (see chapter 2).

This hypothesis may provide a tentative explanation for the contrast effect observed in these experiments. A reduction in the activity and an increase in the latency of transient mechanisms may occur with decreasing contrast (e.g. Harwerth & Levi, 1978), resulting in increased persistence duration. Contrast has been shown to affect both the amplitude and latency of early components of the VEP to gratings (Kulikowski, 1977a). These early components may represent the activity of cortical transient mechanisms. Their latency decreased linearly with increasing log contrast, being reduced by about 40 msec as contrast increased from about 0.02 to 0.7. Parallel relationships were observed for spatial frequencies ranging from 5 - 15 c/deg.

This latency x log contrast relationship resembles the persistence x log contrast relationship observed in Experiment 2. In this experiment, persistence decreased by 40 - 60 msec over a similar contrast range for spatial frequencies of 1 and 4 c/deg. The similarity between these relationships may thus indicate that increasing contrast affects the persistence duration of low frequency gratings by decreasing the latency of transient off-responses.

Legge (1978) has shown that sustained activity occurs at spatial frequencies as low as 1 c/deg, and that this can account for the detection of grating signals in the absence of transient activity. Therefore, sustained activity persisting after the offset of low contrast gratings as a result of delayed transient off-responses may account for the longer

persistence durations of low contrast levels of low frequency gratings.

With the 12 c/deg grating a linear relationship between persistence and log contrast was not observed. This may be due to some extent to experimental artifacts as discussed previously. The difference in this relationship may also indicate that, at higher spatial frequencies, transient activity is minimal at intermediate contrast levels. Although Kulikowski and Tolhurst (1973) indicate that transient mechanisms may respond to spatial frequencies as high as 30 c/deg, it is possible that they require considerably higher contrast levels to reach threshold at these frequencies than at lower spatial frequencies. The lack of any effect of contrast upon the persistence of the 12 c/deg grating at intermediate contrast levels may thus indicate that transient off-responses are below threshold at these contrasts. Persistence duration may be entirely determined by the duration of the sustained response. At high contrast levels the accelerated decline in the 12 c/deg contrast x persistence relationship may indicate that transient mechanisms are now above threshold. A rapid decrease in the latency of these off-responses with increasing contrast may consequently occur.

The possible effect of transient off-responses on persistence may also explain the adaptation results of Meyer et al. (1975) and Meyer (1977). Adaptation to stationary high contrast stimuli appears to have a disinhibiting effect upon transient activity (Georgeson, 1976a, b). This increased transient activity would presumably have a greater inhibitory effect on sustained activity (Singer & Bedworth,

1973), resulting in decreased persistence.

The contrast effect demonstrated in this chapter may be of cortical origin as the comparison with Kulikowski's (1977a) VEP data would perhaps suggest. In addition, a linear relationship between response amplitude and the logarithm of the contrast of gratings has been observed in simple cortical neurones of cats (Maffei, 1978). Neither retinal nor geniculate cells showed such a relationship. Contrast may thus be processed at the cortical level.

Alternatively, it is possible that the visual system responds to changes in contrast in a similar manner to that in which it responds to changes in luminance. Persistence duration decreased linearly by approximately 90 msec with an increase in luminance of 4 log units (Efron, 1970c). Efron's data indicate that this luminance effect is probably peripheral since it was demonstrated to occur in the first persistence component. (No second component was present under the conditions of this experiment). Contrast may thus affect persistence at a peripheral level of the visual system.

These alternative explanations for the contrast effect and the location of the responsible mechanism will be considered in more detail in chapter 6.

CHAPTER 5

THE EFFECT OF STIMULUS DURATION UPON PERSISTENCE

It was shown in chapter 4 that the persistence duration of gratings increases with increasing spatial frequency. The relationship between persistence and spatial frequency was similar to that between critical duration and spatial frequency observed by Legge (1978). The experiment reported in the present chapter further investigates this similarity between persistence and critical duration. This was done by measuring the persistence of gratings of three different spatial frequencies across a range of stimulus durations.

Several experiments in which persistence has been investigated as a function of stimulus duration have shown that persistence initially declines linearly with increasing stimulus duration (e.g. Efron, 1970a, c; Haber & Standing, 1970). The apparent duration of the stimulus remains constant for stimulus durations ranging from near zero to over 100 msec. The slope of the relationship between persistence and stimulus duration is thus approximately -1.0 at brief stimulus durations (Efron, 1970a, c). With stimulus durations exceeding 100 - 200 msec, however, either negligible persistence is observed (Efron, 1970c), or the duration of persistence remains constant with increasing stimulus duration (Efron, 1970a). The persistence x duration relationship consequently changes slope at a stimulus duration called the 'critical duration' by Efron (1970a). This was about 130 msec in Efron's experiments. Haber and Standing (1970), using a letter array stimulus and light pre- and post-adapting

fields, obtained data which indicate that the 'critical duration' is approximately 200 msec under these conditions.

Data obtained by Di Lollo (1977) and Di Lollo and Wilson (1978) also indicate that an inverse relationship between persistence and stimulus duration exists for stimulus durations of 100 - 120 msec when the stimuli are light pulses presented against a dark background. The maximum stimulus duration for which this relationship holds is similar to the critical duration of time-intensity reciprocity under low illumination levels. It was hypothesised in chapter 2 that this inverse relationship between stimulus duration and persistence is due to the limited temporal resolution of the visual system, the response to a brief stimulus persisting because it is "smeared" over the period of temporal integration of the visual system. Consequently, at least one component of persistence may be identified with temporal integration.

The results of Experiment 1 have shown that persistence duration is considerably longer than the critical duration, indicating that factors other than integration time may also contribute to persistence. Appreciable persistence may also be observed for stimulus durations exceeding the critical duration under some circumstances (Efron, 1970a). A second persistence component, possibly occurring at the cortical level, was thus hypothesised to exist. The relationship between these persistence components was depicted in Figure 1.

5.10 Experiment 5

The above hypotheses were tested by investigating the effect of stimulus duration on persistence under circumstances in which the integration time of the stimuli could be manipulated. This was done by varying the spatial frequency of the gratings, since critical duration increases with increasing spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978). It was hypothesised that the stimulus duration wher the change in the slope of the persistence x duration relationship occurred would be similar to the threshold critical duration of each spatial frequency. This stimulus duration will be called the 'intersection duration' rather than the 'critical duration' (Efron, 1970a) to distinguish it from the critical duration of time-intensity reciprocity at threshold. The intersection duration was expected to increase with increasing spatial frequency.

The persistence durations of gratings varying in spatial frequency were consequently measured for a range of stimulus durations. Two linear regression lines were fitted to the data for each spatial frequency and the intersection durations obtained from these were compared with critical duration data of Legge (1978).

Method

Apparatus. The stimuli were presented by means of a Scientific Prototype 3 Channel tachistoscope (Model GB). The stimuli were three photographic reproductions of oscilloscope generated sinusoidal gratings subtending spatial frequencies 1, 4 and 12 c/deg at a contrast of 0.44. The space-average luminance of the gratings and of the blank with which they

alternated was kept constant at 9 cd/m^2.

Subjects. These were twelve volunteers, predominantly post-graduate students and staff of the Psychology Department. Several had participated in the previous experiments but the task was new to a number of subjects. All had normal, or corrected-to-normal vision.

Procedure. Persistence was measured in the same manner as described in chapter 4. The grating stimulus was alternated with a blank ISI for 10 cycles. The duration of the ISI was varied in 10 or 20 msec steps and subjects were asked to report whether a distinct blank interval was visible between each grating cycle. A double random staircase method was employed (Cornsweet, 1962). For each block of trials, the initial ISIs of the ascending and descending staircases were chosen so that they were 100 msec apart. The blank was not visible at the initial ISI of the ascending staircase and clearly visible at the initial ISI of the descending staircase. A few initial trials were generally necessary to establish these starting points. Six threshold reversals were obtained in each block of trials.

A total of 18 blocks of trials, each of which comprised one stimulus condition, was performed on each subject. Each stimulus condition comprised one of the three spatial frequencies (1, 4 and 12 c/deg) at one of 6 durations (50, 75, 100, 150, 200, 300 msec). Two experimental sessions of approximately an hour's duration were employed. An initial practice block of trials preceded the experimental blocks in each session. The order of presentation of the stimulus conditions was randomised with the constraint that conditions

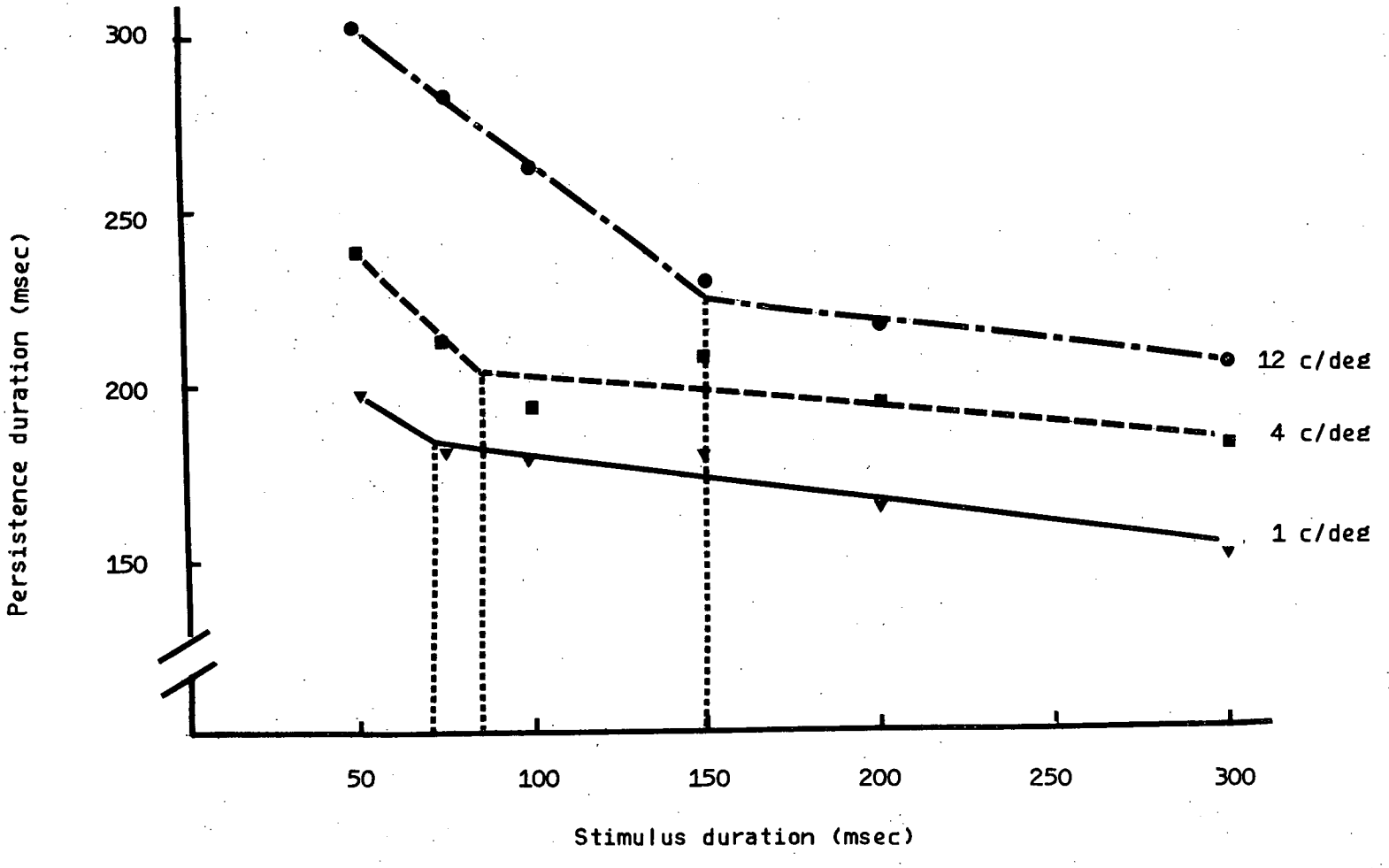

Figure 7. The relationship between stimulus duration and the persistence of 1, 4 and 12 c/deg gratings. The intersection duration is obtained from the points of intersection of the two regression lines.

involving each spatial frequency were separated from each other by conditions involving the other two spatial frequencies. This was to minimise possible adaptation effects.

Results

The data are shown in Figure 7. For each spatial frequency, a decline in persistence duration was observed with increasing stimulus duration. The analysis of variance indicated that the main effect of duration was highly significant ($F(5,55) = 17.08$, $p < 0.001$). A highly significant spatial frequency effect was also observed ($F(2,22) = 56.64$, $p < 0.001$). Longer persistence was observed at higher spatial frequencies for all stimulus durations. A significant spatial frequency x duration interaction ($F(10,110) = 3.02$, $p < 0.01$) indicated that the rate of decline of persistence with increasing duration differed across spatial frequencies. Two linear regression lines were fitted to the data for each spatial frequency by the method of least squares. The stimulus durations and persistence values of the points of intersection of the two lines were obtained.

These values, together with the slopes of the regression lines are given in Table I. There is some variation between the slopes for the different spatial frequencies (see Fig. 7) but these do not appear to follow a regular pattern. The mean initial slope over the three spatial frequencies was -0.75 and the mean secondary slope was -0.13. The values of the intersection duration derived as indicated in Fig. 7 were plotted against spatial frequency (Fig. 8). A linear relationship between intersection duration and spatial frequency

TABLE I

The slopes of the linear regression lines fitted to the data from Experiment 5, and the intersection durations for each spatial frequency.

SPATIAL FREQUENCY (c/deg)	SLOPE		INTERSECTION DURATION (msec)
	INITIAL	SECONDARY	
1	-0.62	-0.14	60
4	-0.89	-0.09	88
12	-0.74	-0.16	152

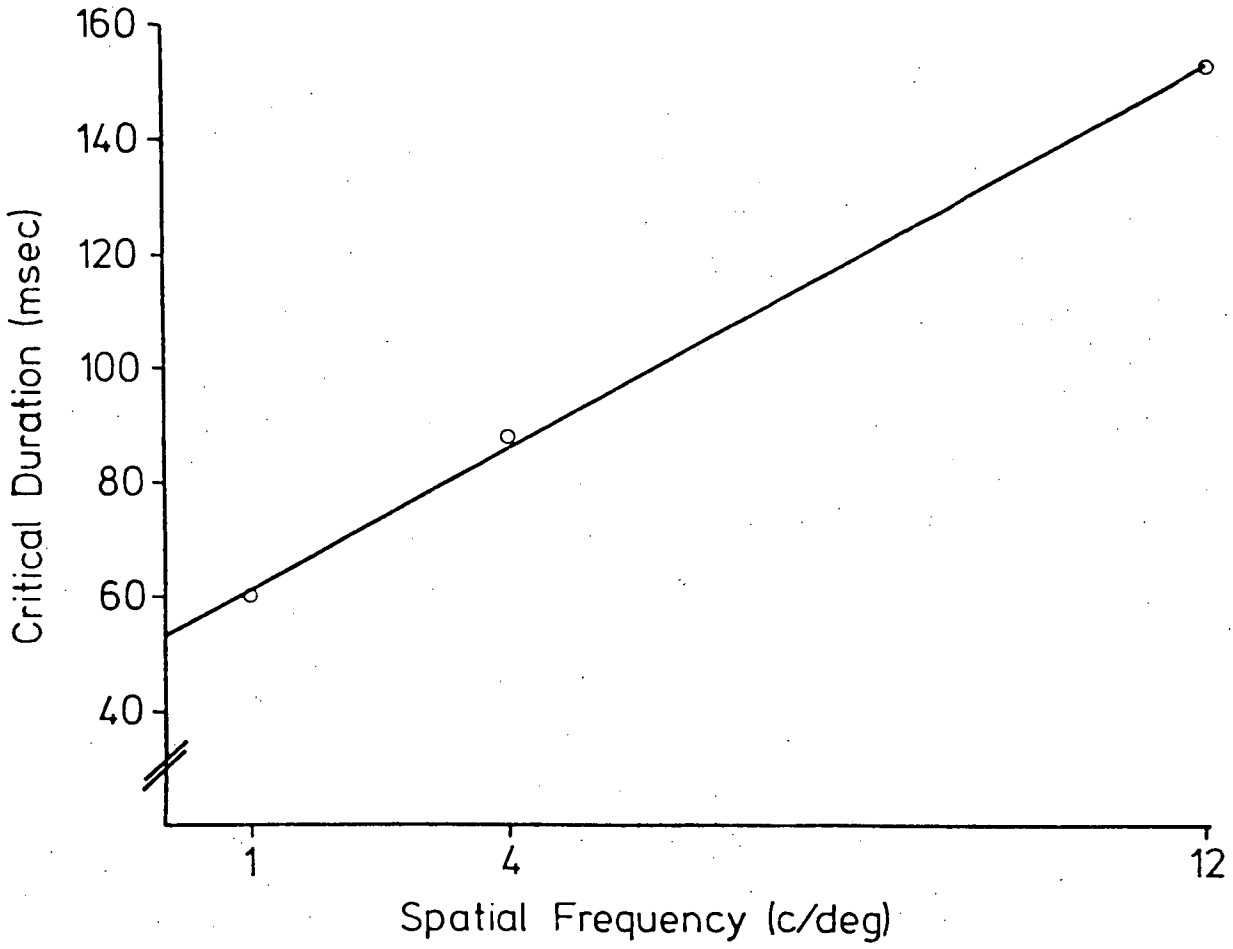

Figure 8. The stimulus durations at the points of intersection of the two regression lines describing the persistence - duration relationships as a function of spatial frequency.

with a slope of 8.3 was obtained.

It is possible that a non-linear continuous relationship may provide a better fit to this data than the two limb linear function depicted here. This possibility was checked by fitting linear, quadratic and logarithmic functions by the method of least squares. The sums of the squared deviations of the data points from each of these regression relationships and from the two limb linear function were calculated. Table II indicates that, for each spatial frequency, the deviation of the data points from the two component linear relationship was lower than that for any other relationship. The two limb linear function is consequently a better fit to the data than any of the other possibilities investigated.

Discussion

The data indicate that the persistence of briefly presented gratings declines linearly with increasing stimulus duration for each spatial frequency investigated. For long stimulus durations, there was only a shallow decline in persistence with increasing duration. This is consistent with the data of Efron (1970a) and Haber and Standing (1970). The stimulus duration at which the change in the slope occurred (the intersection duration) was found to increase linearly with increasing spatial frequency (see Fig. 8). This increase with increasing spatial frequency is similar to the observed increase in threshold measures of critical duration with increasing spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978) although the values for intersection duration derived in this experiment are somewhat shorter than Legge's (1978) critical duration

TABLE II.

The sums of the squared deviations of the data of Experiment 5 from various possible regression relationships.

	SPATIAL FREQUENCY (c/deg)		
RELATIONSHIP	1	4	12
Linear	98	682	1023
Quadratic	97	550	26
Logarithmic	231	281	393
Two phase linear	43	178	23

values. Critical duration is known to vary with other stimulus conditions such as luminance (e.g. Roufs, 1972a) and may differ for threshold and suprathreshold measurements, and for monocular and binocular viewing conditions (Ueno, 1977b). The observed differences between the values of critical duration obtained by Legge (1978) and the values of intersection duration, thus do not necessarily invalidate the identification of the latter with critical duration. In addition, it is not claimed that these values represent accurate measures of critical duration under the conditions of the experiment, being only approximate estimates of the maximum duration of temporal integration for the three spatial frequencies employed.

The results of this experiment have indicated that persistence duration is dependent to some extent upon the integration time of the visual system and consequently increases under conditions where critical duration is increased. The increased persistence of high frequency gratings observed in this and previous studies (Experiments 1, 4; Meyer & Maguire,1977) may thus be partly due to the increased integration times of gratings of these frequencies. This relationship, however, is also observed when the stimulus durations are considerably longer than the integration times of all three spatial frequencies (see Fig. 7). This indicates that mechanisms in addition to temporal integration must contribute to the spatial frequency dependent increase in persistence.

Further evidence that persistence is dependent upon spatial frequency at long stimulus durations can be obtained

from the study by Corfield et al. (1978) who showed that "grey-out elimination" increased with increasing spatial frequency for stimulus durations of 600-900 msec. The existence of substantial persistence at long durations may be interpreted as indicating that, using the method of measurement reported in this paper, an additional factor (or factors) may contribute to visual persistence apart from temporal integration.

Under the conditions of this experiment, the slope of the initial decline in persistence with increasing stimulus duration was found to be approximately -0.75, instead of -1.0 as expected. This result may have been due to the method of measurement employed, since different subjects tended to adopt very different criteria for detection of the blank ISI. Subjects who indicated that they could identify the blank interval at short ISIs generally showed smaller effects of stimulus duration than subjects who identified blanks at considerably longer ISIs. A supplementary experiment, in which the same procedure was carried out using repeated sessions with a single subject (who adopted a long ISI criterion) indicated that under these conditions the initial slope was much closer to -1.0.

The slope of -0.75 obtained in this experiment may also possibly be explained by comparison with the results of temporal integration experiments of Breitmeyer and Ganz (1977) and Legge (1978). In each of these investigations it was found that perfect temporal integration does not occur when the contrast detection thresholds of grating stimuli are measured. The initial slope of the log contrast x log

duration relationship in these experiments was found to be approximately -0.70 rather than -1.0. The relationship between stimulus duraton (t) and contrast (c) at threshold is thus $cx(t)^{0.70} = k$ (Breitmeyer & Ganz, 1977) rather than $cxt = k$ (Bloch's Law). This would cause integration of short duration stimuli to take place over a shorter period of time than that of longer duration stimuli, resulting in the relationship obtained in this experiment. The slope of -0.75 may thus be due to imperfect temporal integration occurring under the conditions of the experiment.

The results of this experiment are generally in agreement with those obtained by previous investigators when the persistence of stimuli varying in duration was measured. They support the hypothesis that many investigations of persistence apparently include two separate persistence components in the measurement, and that the first of these components may be identified with temporal integration. The nature of the second persistence component will be considered in more detail in the next chapter.

CHAPTER 6

THE EFFECTS OF ORIENTATION, CONTRAST AND LUMINANCE PROFILE ON THE TWO PERSISTENCE COMPONENTS

The data presented in the previous chapter provide some evidence for the hypothesis, outlined in chapter 2, that persistence is comprised of more than one component. The appreciable persistence occurring at long stimulus durations for all spatial frequencies appears to be due to the presence of a second component to persistence. The first persistence component resembles temporal integration since its maximum duration increases with increasing spatial frequency in a way that parallels the spatial frequency dependent increase in critical duration (Breitmeyer & Ganz, 1977; Legge, 1978). Evidence that temporal integration occurs predominantly at peripheral levels of the visual system has been discussed in chapter 2. The first persistence component may consequently arise from integration processes occurring at peripheral levels of the visual system.

The second persistence component appeared to increase persistence duration by 150-250 msec and to decline only slightly with increasing stimulus duration. It is hypothesised that the second component occurs at later stages of visual processing than the first component.

This chapter presents further evidence for the existence of two persistence components by describing experiments in which the effects of varying stimulus parameters were

examined over a similar range of stimulus durations to those employed in Experiment 5. Specifically, the effects of orientation, contrast and luminance profile were investigated.

Meyer et al. (1975) and Meyer (1977) have used an adaptation paradigm to provide evidence that persistence duration may be influenced by cortical processes. Since orientation detectors apparently do not occur in any areas peripheral to the visual cortex (e.g. Hubel & Weisel, 1962), the observed orientation-specific adaptation effects on persistence were presumably due to cortical processes. The adaptation results therefore show that persistence duration may be modified by cortical activity but they do not necessarily indicate that persistence is generated in the cortex (Coltheart, 1980).

Further evidence that the total duration of persistence is affected by cortical processes has been obtained by Lovegrove, Bowling and Gannon (Note 1) who demonstrated that the persistence of oblique gratings is longer than that of vertical or horizontal ones. This observation is consistent with many studies in which differences between the perception of oblique and vertical or horizontal stimuli have been noted (Appelle, 1972). Measurements of the contrast sensitivity of gratings have shown that oblique gratings are less resolvable than vertical or horizontal ones. This difference increases with increasing spatial frequency (Berkley, Kitterle & Watkins, 1975; Campbell, Kulikowski & Levinson, 1966; Lennie, 1974). This "oblique effect" has been shown to depend on retinal rather than

gravitational orientation (Corwin, Moskowitz-Cook & Green, 1977; Lennie, 1974). Physiological studies have shown that the psychophysical results may be due to a bias in the orientation preferences of cortical cells (Fregnac & Imbert, 1978; Leventhal & Hirsch, 1977), or to differences in their tuning properties (Rose & Blakemore, 1974). Larger numbers of cells preferring vertical or horizontal to oblique orientations have been observed in the visual cortices of cats (Fregnac & Imbert, 1978; Leventhal & Hirsch, 1977). This bias appears to be confined to X-like (sustained) cortical cells (Leventhal & Hirsch, 1977).

These physiological results have been supported by a psychophysical study which showed that the oblique effect disappeared as the temporal modulation rate of gratings increased (Camisa, Blake & Lema, 1977). This indicates that the effect may be confined to mechanisms with poor temporal resolving power (sustained mechanisms). Further evidence that sustained mechanisms are predominantly involved may be obtained from observations that the oblique effect is less pronounced at low spatial frequencies (Campbell et al., 1966; Lennie, 1974) and at high retinal eccentricities (Berkley et al., 1975).

The probable localization of the oblique effect in cortical sustained mechanisms indicates that the longer persistence durations of oblique gratings (Lovegrove et al., Note 1) may be the result of prolonged activity at this level. This information enables the characteristics of the two hypothesised persistence components to be investigated further, since orientation differences are only likely to

affect the duration of the component (or components) which occurs in the visual cortex. It is hypothesised that orientation will not affect the first persistence component, which appears to be due to peripheral processes but that it will influence the duration of the second component. The following experiments were designed to test these hypotheses.

6.10 Experiment 6

The experiment of Lovegrove et al. (Note 1) demonstrating a persistence oblique effect was performed using a 50 msec exposure duration where both persistence components would have contributed to total persistence duration. It therefore provides no information about which persistence component is affected by orientation. If persistence is measured at long exposure durations, however, the temporal integration component appears to be minimal. Any effect of orientation on persistence at these durations can consequently be attributed to the second component (see Figure 1). An experiment similar to that performed by Lovegrove et al. (1980) was therefore performed using an exposure duration of 200 msec. This is longer than (or as long as) the critical durations of all spatial frequencies employed (Legge, 1978).

Method

Subjects. These were eight students, the majority of whom were volunteers, although some were obtained through the student employment service and paid $2 per hour. All had normal or corrected-to-normal vision. Many had participated in the previous experiments, but completely inexperienced subjects were given a half-hour practice session prior to the experimental session.

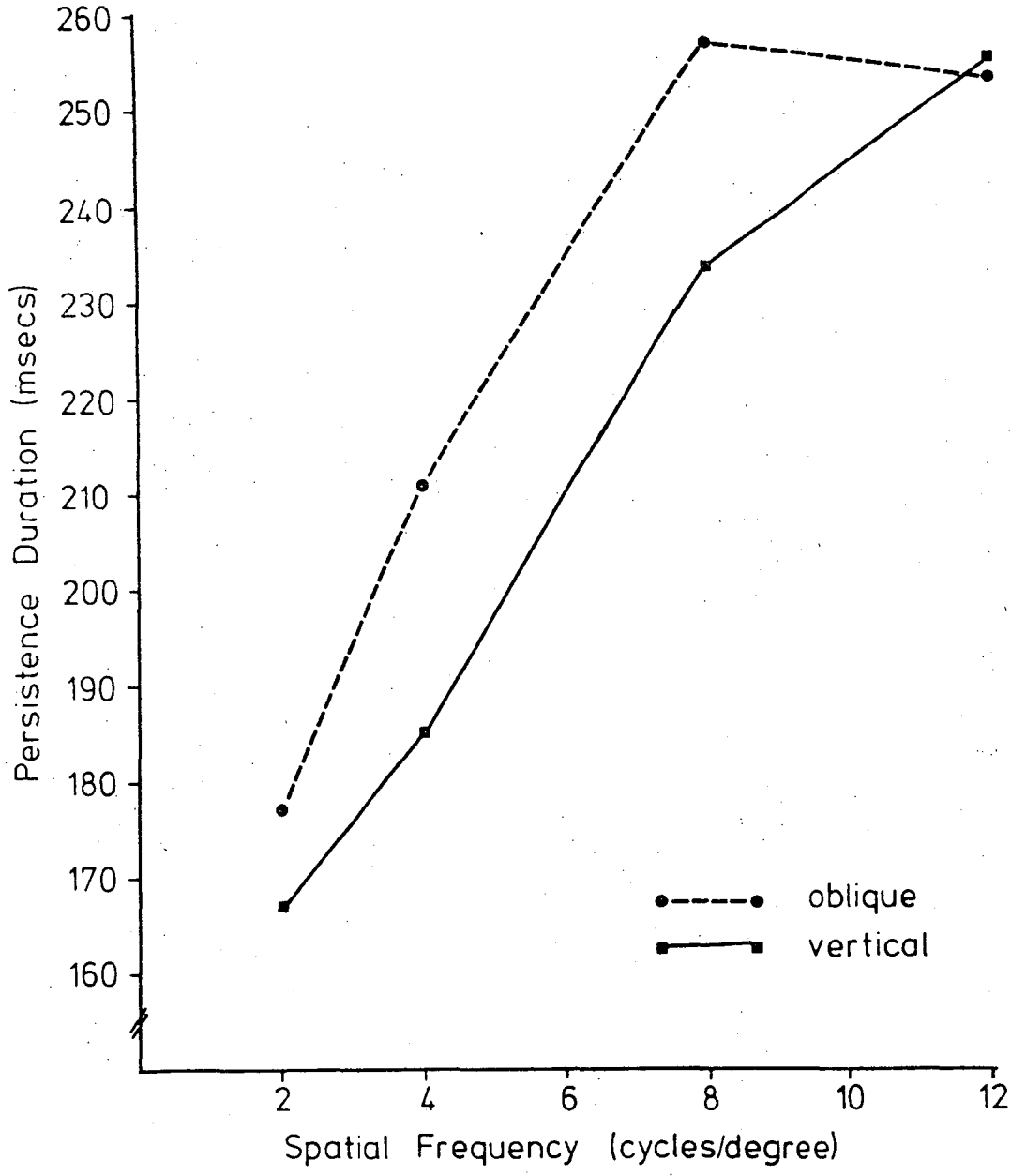

Figure 9. The mean persistence durations of oblique and vertical gratings presented for 200 msec as a function of spatial frequency.

Apparatus. The stimuli were the same photographic reproductions of sinusoidal gratings used by Lovegrove et al. (1980). Vertical and right oblique (top oriented 45^{o} to the right) 2, 4, 8 and 12 c/deg gratings were presented by means of a Scientific Prototype Tachistoscope (Model GB) through a circular field 3.5^{o} in diameter. The Michelson contrast of all stimuli was approximately 0.6, and the luminance of each stimulus and of the blank with which they alternated was kept constant at 7 cd/m^2.

Procedure. The alternating procedure described in chapter 4 was employed. The stimulus was presented binocularly for 200 msec and alternated with a variable duration blank ISI for ten cycles. The random staircase method was similar to that described in chapter 4 but two blocks of trials with 4 threshold reversals each were performed for each experimental condition (4 spatial frequencies at 2 orientations). Although the presentation order of spatial frequencies was counterbalanced across subjects, the oblique and vertical conditions were always presented alternately, to reduce possible adaptation effects. The presentation order of the second sequence of trial blocks was always the reverse of that used for the first to counteract possible gradual changes in criterion. Data were averaged over both trial blocks for each condition for each subject.

Results and Discussion

Mean persistence durations averaged over the 8 subjects are shown as a function of spatial frequency in Figure 9. Persistence lengthened with increasing spatial frequency for both oblique and vertical gratings, although a slight

reduction was observed for the 12 c/deg oblique grating. The spatial frequency main effect was highly significant ($F(3,21) = 12.64$, $p < 0.001$), confirming the previous observation (Experiment 5) that spatial frequency influences the duration of the second persistence component in addition to that of the first.

The persistence durations of oblique gratings were longer than those of vertical stimuli for all spatial frequencies except 12 c/deg. This orientation effect was significant ($F(1,7) = 8.54$, $p < 0.05$). The persistence oblique effect therefore occurs at stimulus durations where only the second persistence component is likely to be present, and it may consequently be concluded that cortical activity may modify the duration of this component. It does not eliminate the possibility that the first persistence component is also influenced by orientation.

6.20 Experiment 7

Experiment 5 has shown that persistence duration relates to stimulus duration in a way that can be explained by a two-component theory of persistence. For brief stimulus durations, persistence decreased with a slope of approximately -0.7 with increasing stimulus duration. It was hypothesised that this steep decline was due to the presence of an integration component to persistence. For longer stimulus durations the rate of decline in persistence with increasing duration was much reduced and this persistence was hypothesised to comprise a second component. The change in the slope of the persistence x duration relationship occurred at approximately the critical duration as obtained from threshold

measures of temporal integration (Legge, 1978). The stimulus duration at which this change in slope occurred was called the 'intersection duration'.

By obtaining the persistence x duration relationships for particular sets of stimulus conditions, the effects of different variables upon the two hypothesised components may consequently be examined independently. The hypothesis that the first persistence component is peripheral and the second central may thus be tested by investigating the effect of orientation upon persistence across a range of durations. If orientation only affects the second component, oblique stimuli would be expected to produce a uniform elevation in persistence across all stimulus durations. No differences between oblique and vertical stimuli intersection durations should occur. In other words, the duration of the first component would be expected to be the same for both vertical and oblique stimuli. This hypothesis was tested in the following experiment.

Method

Subjects. These were a different group of eight individuals obtained in the manner described in Experiment 6.

Apparatus. The oblique and vertical 4 c/deg stimuli described in Experiment 6 were used.

Procedure. The persistence durations of the oblique and vertical gratings were measured as described previously, using exposure durations of 50, 75, 100, 150, 200 and 300 msec. Data were collected in two 3/4 hour sessions for each subject, one trial block (4 threshold reversals) for each condition being run in each session. The order of presenta-

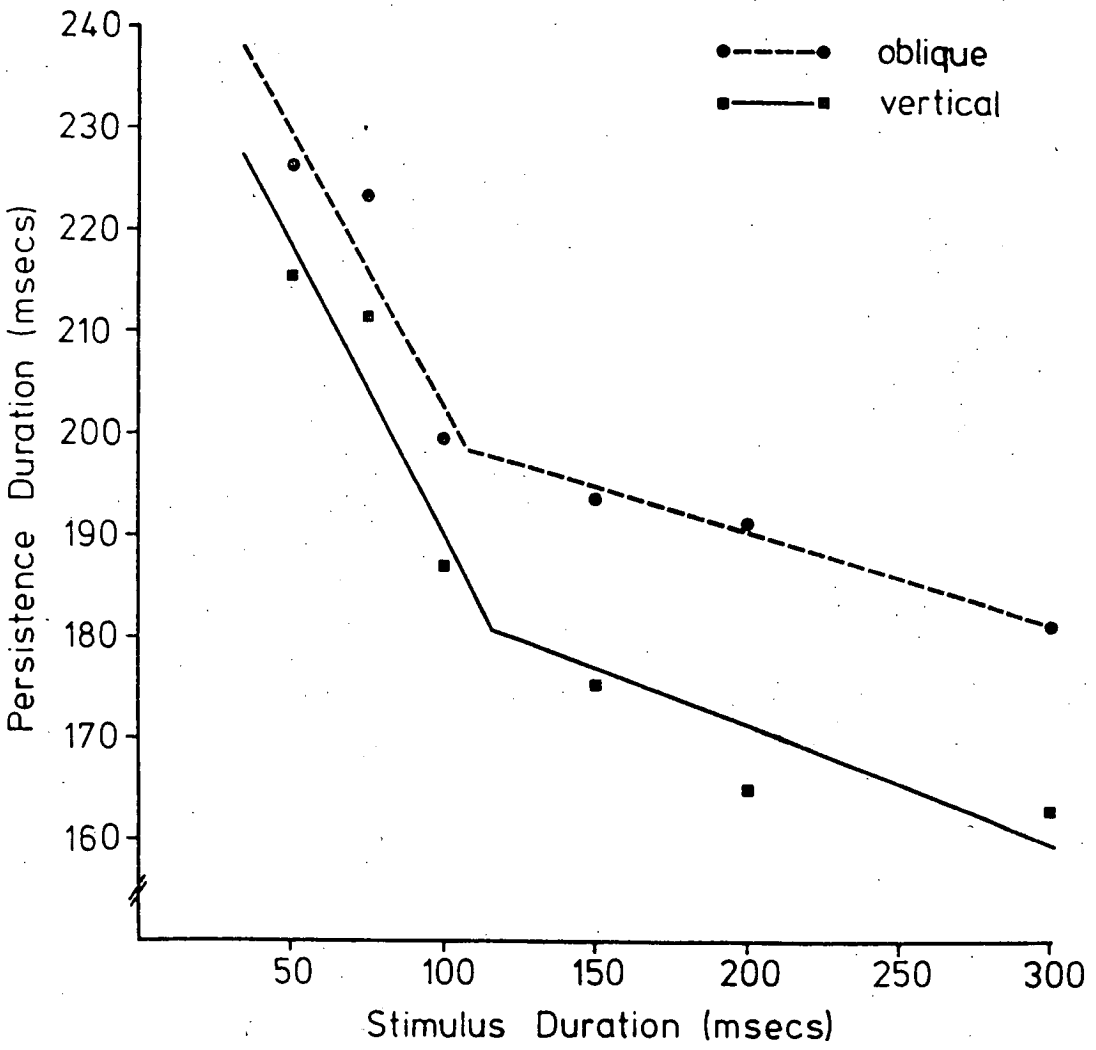

Figure 10. The mean persistence durations of oblique and vertical 4 c/deg gratings as a function of stimulus duration.

tion of each duration was counterbalanced across subjects. Oblique and vertical stimuli were always presented sequentially within each exposure duration.

Results

The mean persistence durations for each orientation are shown in Figure 10 as a function of stimulus duration. The persistence x duration relationship for each orientation has been described by two intersecting straight lines fitted by the method of least squares. Points for inclusion in each segment of the graphs were chosen using the criterion that the slope of the initial steeply declining portion should be maximum. The initial slopes of the relationship were -0.57 and -0.54 for the vertical and oblique gratings and the points of intersection of the two segments occurred at stimulus durations of 116 and 107 msec respectively.

As Figure 10 indicates, oblique 4 c/deg gratings persisted longer than vertical gratings at all exposure durations. An analysis of variance showed that this main effect of orientation was significant ($F(1,7) = 22.3$, $p < 0.01$), and individual t tests showed that this oblique effect was significant at every stimulus duration ($p < 0.05$). The main effect of duration was highly significant ($F(5,35) = 13.2$, $p < 0.001$), but there was no significant orientation x duration interaction ($F(5,35) = 1.4$, $p > 0.05$). There was thus no evidence for a difference between vertical and oblique stimuli in the rate of decline in persistence with increasing duration.

Discussion

The lack of a significant orientation x duration interaction, and the similarity between the intersection durations of the two orientations indicate that the duration of the first persistence component is not affected by orientation. This is as expected from a peripheral temporal integration explanation of the first component. The increase in the persistence of oblique gratings at every stimulus duration is consistent with the hypothesis that orientation affects the second persistence component which therefore appears to be due to cortical processes. It may also be inferred that at least part of the second persistence component occurs subsequent to the first, so that total persistence duration measured by the separation threshold method may be the sum of the two components. The data are thus consistent with a two-component interpretation of persistence, one component of which is peripherally located whereas the other is probably central.

6.30 Experiment 8

It was shown in Experiments 1 and 2 that the visible persistence of low contrast gratings is longer than that of medium or high contrast stimuli. Since this result was obtained at an exposure duration of 50 msec, where both persistence components contribute to total persistence duration, a reduction in contrast may have increased the duration of either the first or second component. It is possible that the duration of Component 1 may be increased by reduced contrast through an increase in integration time, in the same way that a reduction in luminance increases the latter. Alternatively, contrast may affect persistence

duration at the cortical level (see chapter 4). If reduced contrast increases the duration of temporal integration, the following differences between the persistence x duration relationships at low and high contrast levels would be predicted. (1) The longer persistence would only be expected to occur for short exposure durations where both components contribute to persistence. There is some evidence that the contrast effect does only occur at brief stimulus durations, since Corfield, et al. (1978) did not observe any effect of contrast on "grey-out elimination" using stimulus durations of approximately 600-900 msec. (2) The intersection durations obtained with low contrast gratings would be expected to be longer than those of high contrast gratings. If the contrast differences are due to the second component, however, the two relationships should be essentially parallel, with no marked differences between the two intersection durations.

The following experiment was performed to test the hypothesis that a reduction in contrast affects persistence by increasing the duration of the first component. The persistence duration produced by high and low contrast gratings was measured across a range of exposure durations. Vertical and oblique conditions were also included to confirm and extend the results of Experiment 7.

Method

Subjects. Eight subjects were obtained in the manner described for Experiment 6.

Apparatus. The 0.6 contrast vertical and oblique 4 c/deg gratings were again employed, together with approximately 0.1 contrast vertical and oblique gratings of the same spatial frequency. Experiments 1 and 2 have shown that a substantial

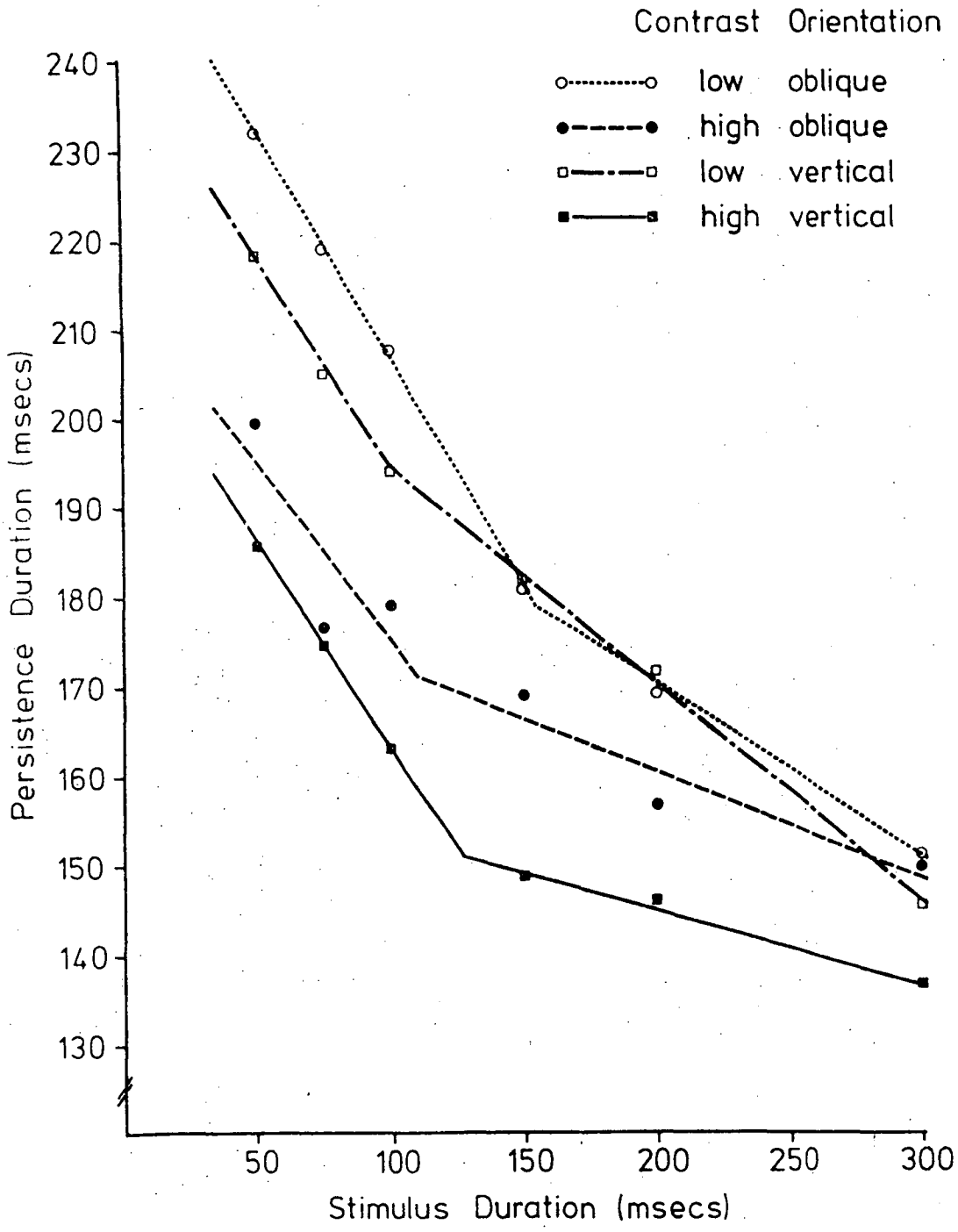

Figure 11. The mean persistence durations of high (0.6) and low (0.1) contrast oblique and vertical 4 c/deg gratings plotted against stimulus duration.

elevation in persistence is produced by the latter contrast level at 4 c/deg.

Procedure. The experiment was conducted over 4 sessions for each subject, with an additional ½ hour practice session being given to inexperienced subjects. The order of presentation of each stimulus duration was again counterbalanced across subjects and at each exposure duration every orientation x contrast combination was run successively. Oblique and vertical stimuli were again presented sequentially. The data for each condition were collected in 2 trial blocks of 4 threshold reversals each. The first blocks for each condition were run in the first two experimental sessions, with the second series of trial blocks being run in the reverse order in the second two sessions.

Results

The persistence results for each orientation x contrast combination are shown as a function of stimulus duration in Figure 11. Two intersecting regression lines have again been fitted to each set of data. The slopes of the regression lines and the estimated intersection stimulus durations are given in Table III. Figure 11 shows that at short stimulus durations low contrast 4 c/deg gratings persisted longer than high contrast gratings, for both oblique and vertical stimuli. At longer exposure durations, however, the effect of contrast was less pronounced, and a reduction in the oblique effect is also apparent with low contrast stimuli.

This data showed significant non-homogeneity of variance and, for this reason, a square root transform was applied prior to analyses of variance. Analyses were performed on the entire

TABLE III

The slopes of the two regression lines fitted to the persistence x duration relationships shown in Fig. 11, and the intersection durations for vertical and oblique 4 c/deg gratings at two levels of contrast.

CONTRAST	ORIENTATION	SLOPES PRIMARY	SLOPES SECONDARY	INTERSECTION DURATION (msec)
High	Vertical	-0.46	-0.08	126
	Oblique	-0.41	-0.12	108
Low	Vertical	-0.49	-0.24	98
	Oblique	-0.51	-0.20	153

data set and separate analyses were also performed on the data at each orientation, and at each contrast level. The overall analysis of variance revealed significant main effects of orientation ($F(1,7) = 8.0$, $p < 0.05$) and contrast ($F(1,7) = 7.9$, $p < 0.05$). A significant contrast x duration interaction was also observed ($F(5,35) = 3.4$, $p < 0.05$) indicating that the degree of persistence elevation due to reduced contrast was dependent upon stimulus duration. The orientation x duration interaction was not significant ($F(5,35) = 0.86$, $p > 0.05$), but a trend towards a significant contrast x orientation x duration interaction was observed ($F(5,35) = 2.21$, $p > 0.05$).

The analyses in which the contrast effect was investigated separately at each orientation revealed that there was a significant contrast effect with both vertical ($F(1,7) = 6.85$, $p < 0.05$) and oblique gratings ($F(1,7) = 9.98$, $p < 0.05$). There was, however, a significant contrast x duration interaction with oblique orientations ($F(5,35) = 4.48$, $p < 0.01$), but not with vertical ($F(5,35) = 1.19$, $p > 0.05$). Examination of Figure 11 shows that the significant interaction obtained with the oblique stimuli is due to a reduction in the effect of contrast upon persistence at stimulus durations of 150 msec and longer. A similar tendency towards a reduction in the contrast effect at long durations was also evident with the vertical data, but it did not occur at any stimulus duration shorter than 300 msec. A reduction in the contrast effect as duration increased was therefore observed for both vertical and oblique gratings, but was more obvious for the oblique orientation. For both orientations, the slopes of the secondary regression lines

were somewhat steeper with low than with high contrast stimuli (see Table III).

The results of the analysis of variance of the high contrast data may be compared with the results of Experiment 7. The analysis revealed a significant orientation main effect ($F(1,7) = 8.2$, $p < 0.05$), but no significant orientation x duration interaction. The intersection durations were 126 and 108 msec for vertical and oblique orientations respectively. A similar analysis of the low contrast data showed that neither orientation ($F(1,7) = 3.5$, $p > 0.05$), nor the orientation x contrast interaction ($F(5,35) = 1.42$, $p > 0.05$) were significant.

Discussion

The results of this experiment have shown that the persistence durations of low contrast 4 c/deg gratings are longer than those of high contrast gratings, especially at short exposure durations. The contrast effect is small at long stimulus durations, especially with oblique stimuli. For exposure durations less than 100 msec the persistence x duration relationships were approximately parallel at both contrast levels (see Table III), but at durations longer than this a difference between the slopes of the two functions becomes apparent. The reduced contrast effect at long stimulus durations (Corfield et al., 1978) may consequently be due to a reduction in the effect of contrast on the second persistence component as stimulus duration increases. The significant contrast x duration interaction obtained from the overall analysis of variance may consequently be attributed to the differences in the slopes of the secondary regression line, rather than to possible differences between intersection durations of the two functions. There are some differences between these durations as is obvious from Figure 11. The difference in

intersection durations between high and low contrast stimuli, however, occurs in opposite directions for vertical and oblique stimuli. There is consequently no consistent evidence for an increase in the duration of Component 1 with decreased contrast. Although it cannot be concluded that contrast does not affect the duration of the first component, Figure 11 indicates that contrast predominantly affects the second component.

Since the results of the previous experiment suggest that the second persistence component may result from cortical processes, it appears that the main effect of contrast on persistence may occur in the central rather than in the peripheral visual system. This is in agreement with observations that the magnitude of single cell responses is systematically related to contrast level only in cortical neurones (Maffei, 1978). Of the two alternatives for mechanisms producing the contrast effect outlined in chapter 4, the evidence presented in this chapter thus favours the cortical one. It is unlikely that the contrast and luminance effects are produced by the same mechanisms since luminance probably affects persistence at the peripheral level.

It was hypothesised in chapter 4 that the increase in persistence with a reduction in contrast may be due to an increase in the response duration of sustained cells because of reduced inhibition from transient off-responses. It is possible that a delay in the transmission of transient off-responses occurs with low contrast gratings (e.g. Kulikowski, 1977a) lengthening persistence.

The tendency for the contrast effect to disappear with increased exposure duration is in agreement with the results of Corfield et al. (1978) who found no effect of contrast when stimulus durations of 600-900 msec were employed.

The results of the comparison between vertical and oblique stimuli analysed at the high contrast level are substantially in agreement with the results of Experiment 7. There was a larger difference between intersection durations (18 msec) than in the previous experiment, but the lack of a significant interaction indicates that this difference is most likely due to variability in the data. This is especially noticeable in the oblique condition.

The failure to obtain a significant oblique effect in the analysis of the low contrast data may be due to the greater difficulty subjects experienced in making judgements with low contrast stimuli, and the consequent increase in the variability of the data. It may also indicate that there is a form of ceiling effect occurring - persistence may be lengthened by either low contrast or oblique orientations but not both. There is, however, a small oblique effect at short stimulus durations at low contrast levels (individual t tests comparing vertical and oblique means for the 50, 75, and 100 msec conditions were all significant). An interaction between the mechanisms involved in the oblique effect and those involved in the contrast effect may possibly explain the differences between oblique and vertical stimuli in the contrast effect.

6.40 Experiment 9

The results of the previous experiment have shown that the effect of contrast upon persistence decreases with increasing stimulus duration. The failure of Corfield et al. (1978) to find any effect of contrast on critical-blank-duration in their experiments may consequently be due to their use of long stimulus durations. A further result obtained by Corfield et al. (1978) was that square wave gratings produced shorter critical-blank-durations than sine wave gratings at all spatial frequencies investigated. This finding was unanticipated, since the higher harmonic content of the square wave gratings was expected to increase critical-blank-duration. Previous results had shown that critical-blank-duration was longer with high spatial frequency gratings than with low frequency stimuli.

Pilot data indicated that, under the conditions of persistence measurement described in this thesis, there was no difference between the persistence durations of sine and square wave gratings at 50 msec stimulus durations. It is possible, however, that like the effects of contrast, the presence of higher harmonics in a stimulus may have varying effects upon persistence duration depending upon stimulus duration. The following experiment was consequently designed to compare the persistence durations of sine and square wave gratings at a number of stimulus durations.

The spatial frequency of the sine and square wave gratings used in this experiment was 4 c/deg. A 4 c/deg grating contains a fundamental 4 c/deg sinusoidal component and a 12 c/deg third harmonic together with further higher harmonics.

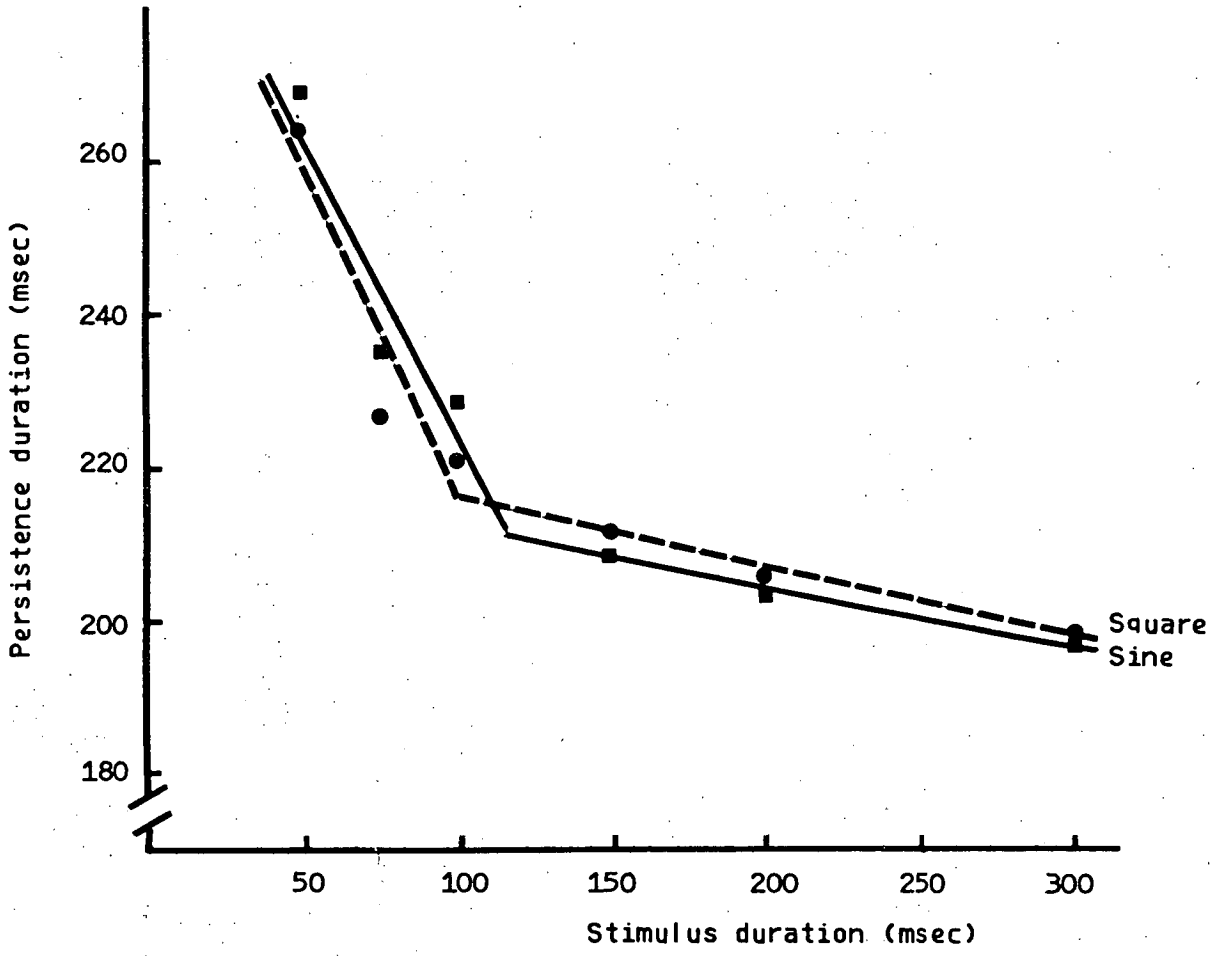

Figure 12. The mean persistence durations of square and sine wave 4 c/deg gratings plotted against stimulus duration.

The contrast of the third harmonic is one third that of the fundamental. The fundamental and third harmonic appear to be analysed independently, at least at threshold (e.g. Campbell & Robson, 1969). The spatial frequencies of the fundamental and third harmonic should be sufficiently different to individually produce considerable differences in their persistence durations and the contrast of the third harmonic should be above threshold at the high contrast levels employed in this experiment.

Method

The method was identical to that of Experiment 7, except that high contrast (0.6) sine and square wave gratings were employed as stimuli.

Results and Discussion

The results of this experiment are shown in Figure 12. The figure indicates that any differences between the two gratings in persistence duration were small at every stimulus duration. There was no significant difference between the persistence durations of sine and square wave gratings ($F(1,7) = 0.20$, $P > 0.05$), nor was there a luminance profile x duration interaction ($F(5,35) = 0.84$, $P > 0.05$). The intersection durations for the sine and square wave gratings were 100 and 116 msec, and the initial slopes of the relationships were -0.75 and -0.87 respectively.

These data indicate that there were no differences between the persistence durations of sine and square wave gratings at any stimulus duration. This result may indicate that persistence duration is determined by the low frequency components of complex stimuli, rather than by the

high frequency components. The results of this experiment are thus contrary to those of Corfield et al. (1978). This discrepancy may be due to the difference between the luminance levels employed in the two experiments. Corfield et al. (1978) used 100 cd/m^2, whereas the current experiment was conducted at a luminance of $7cd/m^2$.

6.50 Experiment 10

Experiments 6 and 7 have provided evidence that the persistence oblique effect occurs within the second persistence component. There was no evidence that differences in orientation had any effect on the duration of the first component, which has been hypothesised to occur as a result of temporal integration. Since temporal integration is thought to occur predominantly at more peripheral locations in the visual system, no orientation effect on this component was anticipated.

The evidence that temporal integration is a peripheral process has been obtained from physiological studies (e.g. Levick & Zacks, 1970), and from forward and backward masking results (see chapter 2). Masking by integration does not normally occur dichoptically (e.g. Turvey, 1973). Long (1979a) has recently argued that demonstrating that an effect occurs dichoptically does not necessarily prove that the effect is due to cortical processes. He considers that a demonstration of the involvement of orientation specific mechanisms would be more powerful evidence for the cortical location of an effect. If cortical mechanisms contribute to the duration of temporal integration of gratings, differences in integration times between oblique and vertical stimuli may consequently be expected. Lack of such differences imply that integration

occurs in the periphery.

Foley (1962) has measured the integration times of stimuli varying in orientation using a critical flicker frequency technique. It was found that, although the critical flicker frequencies were always lower with oblique than with vertical stimuli, the relevant area and luminance functions were parallel, indicating that there were no differences in temporal integration times. An alternative method of measuring the duration of temporal integration is to obtain the critical duration of time-intensity reciprocity threshold. In the current experiment, therefore, the critical durations of vertical and oblique stimuli were measured. Since the stimuli were gratings, critical duration was obtained from a plot of the log contrast by log stimulus duration (Breitmeyer & Ganz, 1977; Legge, 1978). Perfect reciprocity does not occur when contrast, rather than intensity, is the dependent variable.

Method

Subjects. Eight volunteer subjects were recruited from undergraduate and graduate psychology students.

Apparatus. Stimuli were the vertical and oblique 4 c/deg high contrast gratings used previously. Stimuli were presented with the Scientific Prototype tachistoscope through a circular field which was 3.5^{o} in diameter. The grating stimulus was placed in field 1 of the tachistoscope and blank cards were positioned in fields 2 and 3. Polarizing filters of opposing polarities were placed in fields 1 and 2. A third polarizing filter was positioned at the viewing end of the tachistoscope and mounted so that it could be easily rotated by the subject. Rotation of this filter through

90^{o} caused the combined stimulus from fields 1 and 2 to change from a clear blank field at 0^{o} to a high contrast grating at 90^{o}. The luminances of fields 1 and 2 were each adjusted to 1.5 cd/m^2 with the rotating polaroid at 0^{o} and 90^{o} respectively. Rotation of the polaroid consequently changed the contrast of the stimulus without changing its space-average luminance. A neutral density filter was placed in the third tachistoscope field and luminance adjusted to 1.5 cd/m^2. This field provided the background against which the adjustable contrast stimulus was presented, and was illuminated continuously except during stimulus presentation. The small size of the rotating polaroid necessitated monocular presentation for this experiment.

Procedure. The threshold contrast of the two stimuli was measured for exposure durations of 10, 20, 40, 60, 80, 100, 150, 200, 300, 500 and 1000 msec using the method of adjustment. For each duration, the stimulus was presented repeatedly at 1 sec intervals until subjects indicated that they had completed the threshold adjustment. Subjects were given as long as they required for this. Alternate trials commenced with the grating contrast well above, or well below, threshold. When starting from below threshold subjects were asked to rotate the polaroid until they could just detect the grating, and when starting from above threshold, to adjust it until they just failed to see the grating. Four threshold adjustments were made for each stimulus duration, two starting from above threshold, and two from below. The order of presentation of the stimulus durations was random except that data were obtained once at every duration before commencing the second and subsequent trials at any duration. This

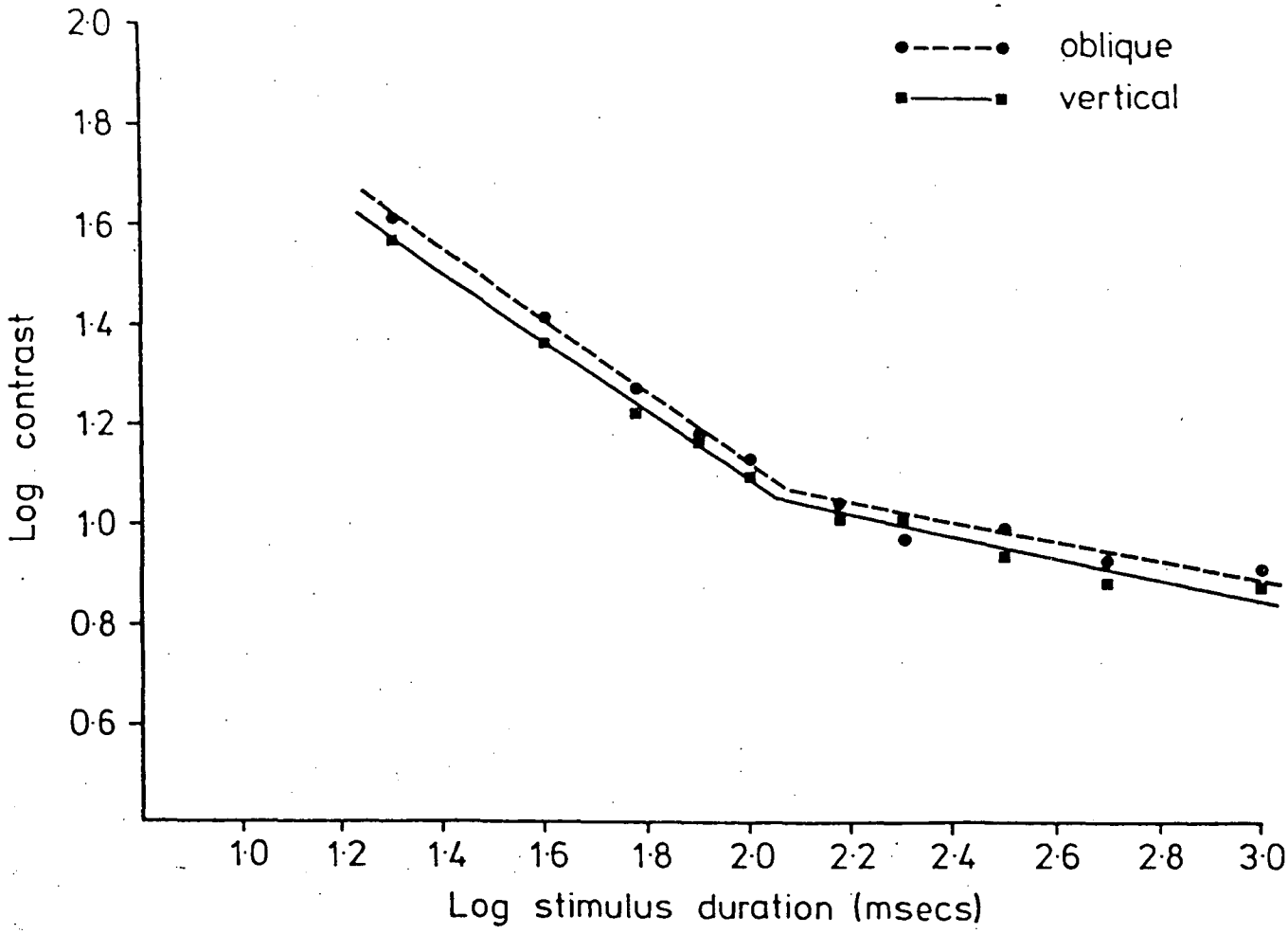

Figure 13. The log mean threshold contrast of oblique and vertical 4 c/deg gratings averaged over 8 subjects, plotted against log stimulus duration.

was to enable any order effects to be distributed evenly across conditions. The data for each orientation were collected separately, with the order of presentation of orientations being counter-balanced across subjects. The data for each subject were collected in a single 1-1½ hour experimental session, with a short break being allowed between the two orientation conditions.

Results and Discussion

For each subject, the orientation of the rotating polaroid was measured and averaged over the four theshold determinations for each condition. This was converted to a contrast value from the formula: contrast = $\sin^2 \theta$. The logarithm of this value (multiplied by 100) was plotted against log stimulus duration, and critical durations for the oblique and vertical gratings were obtained for each subject separately. Mean critical duration for oblique and vertical stimuli, and the mean slope of the two segments of the regression lines fitted to the data are given in Table IV. The threshold data averaged over the 8 subjects are illustrated in Figure 13.

For all except one subject, the contrast detection thresholds with oblique gratings were higher than with vertical gratings at all exposure durations, confirming the presence of an "oblique effect" (Appelle, 1972). The difference between the log contrast detection thresholds was approximately constant across all exposure durations, although the secondary slope of the relationship for the oblique grating was significantly less steep than that for the vertical grating ($t(7) = 2.77$, $p < 0.05$),

TABLE IV

The mean values of the critical durations and primary and secondary slopes of the log contrast x log duration relationships for vertical and oblique 4 c/deg gratings at threshold.

	SLOPES		
ORIENTATION	PRIMARY	SECONDARY	CRITICAL DURATION (msec)
Vertical	-0.74	-0.23	124.3
Oblique	-0.75	-0.18	123.6

There was no evidence for a difference between the mean critical durations of oblique and vertical gratings ($t(7) = 0.04$, $p > 0.05$). Although the contrast detection thresholds of oblique gratings were higher than those of vertical gratings, there was consequently no evidence for any difference in integration times between the two orientations. The evidence thus suggests that although cortical orientation selective mechanisms may be operative in threshold detection tasks they do not affect the duration of temporal integration. The data thus do not provide any evidence that the critical duration measure of temporal integration is a cortical phenomenon. Not all cortical mechanisms show an orientation bias, however (Camisa et al., 1977; Leventhal & Hirsch, 1977), and therefore the possibility that some cortical activity may be involved in temporal integration cannot be entirely eliminated. It is possible that cortical transient cells play some role in determining the duration of temporal integration. Although the data obtained in this experiment are consistent with the hypothesis that temporal integration occurs in the peripheral visual system, it consequently does not eliminate the possibility that transient mechanisms in the visual cortex may also be involved.

Critical duration data have been obtained by Legge (1978) for a range of spatial frequencies. From a linear plot of this data against spatial frequency, a critical duration value of about 130 msec may be estimated for 4 c/deg. This agrees well with the value obtained in this experiment. Similarly the agreement between the initial slopes is good, Legge's mean of -0.72 averaged across all spatial frequencies being similar to the mean initial slope of -0.75 reported here.

Breitmeyer and Ganz (1977) also reported a similar slope (-0.70). A striking aspect of the data was the consistency of this initial slope from subject to subject. The values of the secondary slope were found to be more variable, but they were consistently less steep than Legge's values with higher spatial frequencies.

General Discussion

The two component theory of persistence has been supported by the experiments described in this chapter. Two different mechanisms apparently operate to produce persistence as measured by the method described, and different variables appear to influence these two mechanisms differently. Spatial frequency affects the duration of both components (Experiment 5) whereas contrast and orientation appear to mainly affect the duration of Component 2.

Persistence Component 1 has been considered to be due to the prolonged nature of peripheral neural responses. The evidence presented in ths chapter indirectly supports this hypothesis. Orientation affected neither the duration of temporal integration at threshold nor the duration of the first component. In addition, the value of the critical duration obtained with the 4 c/deg gratings at threshold in Experiment 10 (124 msec) is similar to the duration of Component 1 estimated from the averaged 4 c/deg data shown in Figure 14 (100 msec). Similar experimental conditions were employed for all experiments with the exception that the insertion of polarizing filters made it necessary to reduce the luminance of the stimuli in Experiment 10. Since critical duration increases with decreasing background luminance (e.g. Roufs,

1972a) the greater value of critical duration obtained in Experiment 10 is not unexpected. The similarity between the two measures is good evidence that both are estimates of the duration of the same underlying phenomenon.

The existence of persistence Component 2 may only be detectable with the method of measurement described above. Appreciable persistence is not always observed at long durations when indexing stimuli are used to measure the apparent onset and offset of a stimulus (Coltheart, 1980), or when measurements are made of the duration of the interval over which two or more separate stimuli are integrated (e.g. Di Lollo, 1977; Di Lollo & Wilson, 1978). The question may be raised as to whether it is in fact persistence, since other mechanisms may explain the existence of this component under the experimental conditions described. For example, it may be due to a form of masking in which the successive grating cycles inhibit perception of the blank ISI by acting in both forward and backward directions (e.g. Campbell & Wurtz, 1978). The possibility will be considered in more detail in chapter 8. The fact that the duration of the second component is affected differently by a number of variables does, however, indicate that it is a real phenomenon, and consequently that it is not merely a result of long ISI detection criteria adopted by some subjects.

Assuming that this second component is persistence, the evidence obtained from Experiments 6-8 suggests that it is due to activity in cortical sustained cells, since the bias in orientational selectivity predominates in these (Camisa et al., 1977; Leventhal & Hirsch, 1977). Since

fewer cortical cells respond to oblique than to vertical stimuli, it is possible that cells sensitive to oblique stimuli respond for a longer time period than cells responsive to vertical or horizontal stimuli. This would provide a compensatory mechanism to maximise information extraction. A general trend for weaker stimuli to persist longer than strong stimuli has been observed. This applies to high spatial frequencies, to low contrast stimuli and to oblique orientations, although the mechanisms involved in each case may be different.

The evidence that the contrast effect occurs predominantly in the second persistence component does not necessarily invalidate the previous proposal that low contrast levels may prolong persistence by means of weak or delayed transient off-responses. Retention of this hypothesis means that different mechanisms for the contrast and oblique effects must be proposed, however, since the orientation effect cannot be explained similarly. Differences in orientation apparently do not affect the activity of transient cells (Camisa et al., 1977). The longer persistences of oblique gratings are unlikely to be due to differences in the strength or latency of transient off-responses, but to differences in the response properties of sustained cells. The results of further studies of the possible relationship between transient off-responses and persistence will be presented in chapter 7.

A combination of the properties of both sustained and transient mechanisms may be necessary to determine total persistence duration. An increase in the response time of a sustained cell, or a delay in the arrival of a transient off-

response may both increase the duration of the second persistence component. An upper limit to such an increase may be expected. For example, once a transient response is delayed beyond a certain limit, persistence duration will be determined solely by the response duration of the sustained cells. Some evidence for such an interaction between two mechanisms may be found in the results of Experiment 8.

A comparison of Experiments 5, 7, 8 and 9 indicates that there are differences between the results obtained under similar stimulus conditions. Intersection duration for the vertical high contrast 4 c/deg sine wave grating ranged from 88 msec in Experiment 5 to 126 msec in Experiment 8. The value of the initial slope of the persistence x duration relationship varied between -0.46 and -0.89. These differences reflect individual subject variability, and arise from the difficulty subjects experienced with the task and in maintaining a stable criterion. This variability, together with the relatively few stimulus durations employed, often made it difficult to fit two straight lines accurately to the data. The measures for intersection duration obtained in each experiment were thus only approximate estimates of the maximum duration of Component 1. Small differences in intersection duration between experimental conditions could not be taken as evidence that these differences reflected differing integration times. In addition, it is not always clear that straight lines provide the best fit for the data in all circumstances. The analysis presented in the previous chapter does, however, indicate that other types of

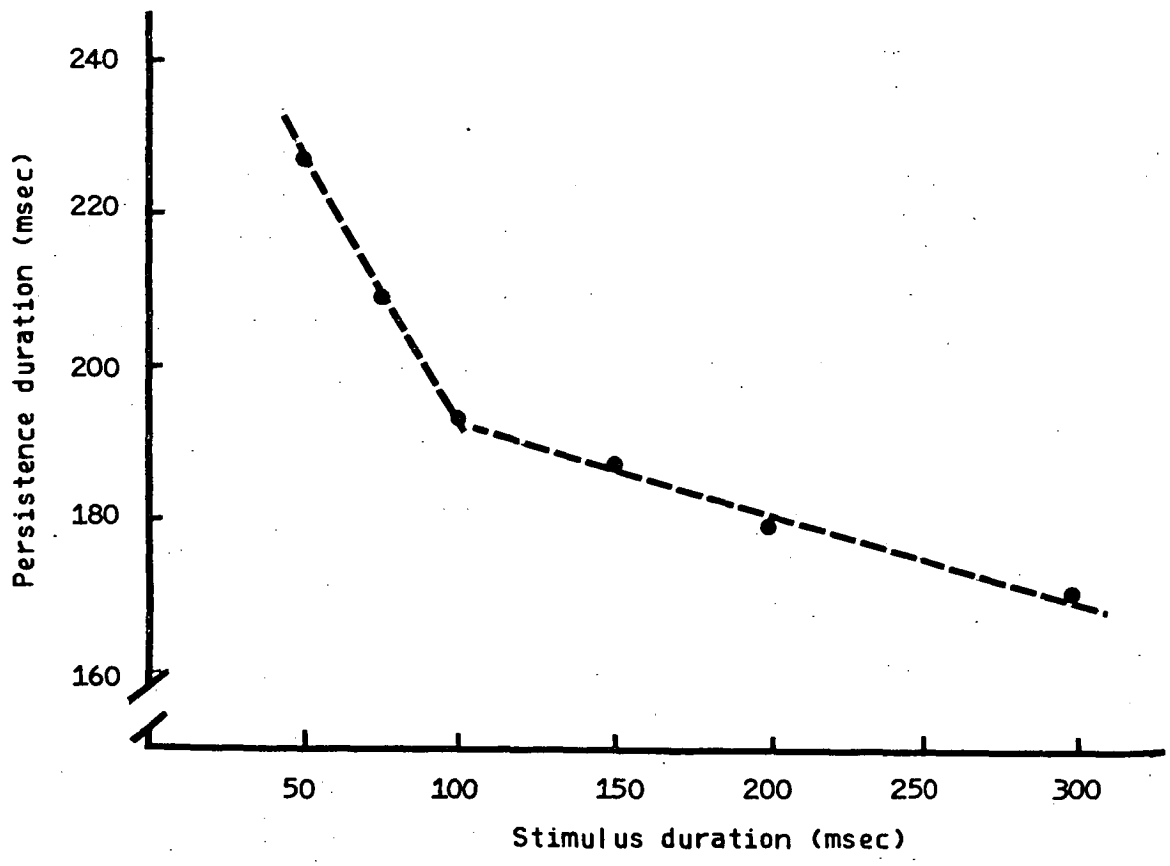

Figure 14. A graph of the data for the mean persistence duration of the high contrast, vertical sinusoidal 4 c/deg grating averaged over a total of 36 subjects from Experiments 5, 7, 8 and 9, plotted against stimulus duration.

functions do not fit the duration data as well as a two-branched relationship.

In order to examine the relationship between persistence and stimulus duration more closely for one stimulus condition, the data for the high contrast vertical 4 c/deg sinusoidal grating from Experiments 5, 7, 8, and 9 were averaged over the total 36 subjects involved. These averaged data are shown in Figure 14 as a function of stimulus duration.

This figure shows that two intersecting straight lines fit thesedata quite accurately. The initial and secondary slopes of these lines are -0.69 and -0.11 respectively, and the intersection duration is 100 msec. The initial slope is similar to the initial slope of the 4 c/deg log duration x log contrast relationship at threshold and the intersection duration is similar to the threshold critical duration (Experiment 10; Legge, 1978). The similarity between the initial slopes of the two relationships provides further evidence for the identification of persistence Component 1 with temporal integration (see chapter 5).

CHAPTER 7

THE EFFECTS OF ADAPTATION ON PERSISTENCE DURATION

It was proposed in chapter 4 that transient off-responses may be responsible for terminating persistence. Recent authors have similarly argued that the strength or latency of transient off-responses may determine persistence duration (Breitmeyer & Kersey, in press; Coltheart, 1980; Long, 1979b). Use of the metacontrast paradigm has provided evidence that the response persistence of sustained cells may be inhibited by transient activity (Breitmeyer, 1980). The demonstration that both mask onset and offset produce metacontrast masking (Breitmeyer, 1978; Breitmeyer & Kersey, in press) indicates that transient off-responses are as effective as on-responses in their inhibitory effects. In metacontrast, however, the transient activity is produced by the masking stimulus rather than by the termination of the target itself.

It was also proposed that the long persistence durations obtained with low contrast gratings may be due to a reduction in the inhibitory effects of transient off-responses. Evidence that the activity of transient mechanisms may decrease with decreasing contrast has been obtained with reaction time methods and from studies with the VEP. These studies were described in chapter 1. Sustained mechanisms apparently determine reaction time at low contrast levels and transient mechanisms at higher contrast levels (Harwerth et al., 1980; Harwerth & Levi, 1978). The amplitude of early

VEP components (possibly transient on-responses) increases, and their latency decreases linearly with increasing log contrast (Kulikowski, 1977a), implying that transient mechanisms respond more vigorously with increasing contrast. Evidence that a reduction in contrast reduces the degree to which the activity of transient mechanisms may inhibit sustained ones may be obtained from an experiment by Michaels and Turvey (1979, Experiment C1). A light grey mask produced less metacontrast masking than a black one, and the difference between the effects of the two masks was greatest at the peak of the metacontrast function. It was hypothesised that 'the black mask, in comparison to masks of lesser contrast, elicits a more potent transient signal and exerts a greater inhibitory effect on the sustained channels' (Michaels & Turvey, 1979, p.24).

These studies together provide reasonable evidence that a reduction in contrast reduces the amplitude and increases the latency of transient on-responses. Similar effects of contrast on off-responses would be expected. If persistence duration is determined by the interval between transient on- and off-responses, however, it is necessary to postulate that decreasing contrast causes off-response latency to increase to a greater extent than on-response latency for contrast to affect persistence. At present there is little evidence for such a differential effect of contrast on latency. Using reaction time procedures, no increase in off-response latency over on-response latency was observed with decreasing contrast (Breitmeyer, Levi & Harwerth, Note 2), or with decreasing luminance (Hansteen, 1971).

This question requires further investigation, as reaction time may not be the most appropriate latency measure.

If transient activity does affect persistence duration this should be influenced by any manipulation which increases or decreases the activity of transient mechanisms. Adaptation to flicker appears to reduce the sensitivity of transient mechanisms (e.g. Tolhurst, 1973) in the same way that the sensitivity of sustained mechanisms is reduced by adaptation to stationary gratings (e.g. Blakemore & Campbell, 1969). Kulikowski (1977b) demonstrated that adaptation to a counterphase flickering 1 c/deg grating considerably reduced the amplitude of the movement (transient) component of the VEP. There did not, however, appear to be any difference in the latency of the response. Petry, Grigonis and Reichert (1979) found that 10 sec of flicker adaptation prior to a metacontrast trial considerably reduced the magnitude of masking, indicating that the inhibitory effect of the mask transient on-response was reduced. This effect was similar to that obtained by Michaels and Turvey (1979) with reduced mask contrast. The graphs of the data of Petry et al. (1979) also indicate that there was a slight increase in the SOA at which maximum masking occurred. The latency of the transient on-response, as well as the reduction in its amplitude, may consequently have been increased by adaptation to flicker. This study shows that the inhibitory effects of transient responses are reduced by adaptation to flicker.

The following experiments were consequently designed to test the hypothesis that persistence duration is influenced

by transient activity. It was hypothesised that adaptation to flickering stimuli would increase persistence duration by reducing the amplitude and possibly increasing the latency of transient off-responses. Subjects were adapted to either a flickering or a steady stimulus prior to each persistence measurement.

7.10 Experiment 11

This experiment investigated the effects on persistence duration of adaptation to both counterphase flickering and stationary gratings. Preliminary investigations showed that adaptation to a flickering 2 c/deg grating produced an elevation in the contrast threshold for detection of the flicker in this stimulus. This contrast threshold elevation was considerably greater than that of the pattern detection threshold of the same stimulus. It was consequently inferred that the flickering adaptation stimulus preferentially adapted flicker, or transient mechanisms rather than pattern, or sustained mechanisms.

Method

Subjects. These were 6 graduate and undergraduate Psychology students. Many had participated in previous persistence experiments.

Apparatus. The Scientific Prototype Tachistoscope described previously was used. It was connected to an interval generator which was necessary for timing the flicker frequency of the flickering adaptation stimulus. Stimuli were two photographic reproductions of approximately 0.6 contrast 2 c/deg gratings. They were aligned in two tachistoscope

fields so that they were 180° out of phase. When alternately illuminated they produced a counterphase flickering grating. Two uniform grey cards were also employed to provide the blank adaptation stimulus and ISI. The luminance of all stimuli was 7 cd/m^2.

Procedure. The persistence of the 2 c/deg grating was measured after adaptation to one of 3 adaptation conditions. These included the counterphase flickering grating alternating at a frequency of 10 Hz, a stationary grating of the same spatial frequency (2 c/deg), and a steady blank field. A variation of the previously described separation threshold method was used to measure persistence. The grating was presented for 80 msec, followed by the ISI and then by a further 80 msec presentation of the same grating. Subjects were requested to indicate whether a clear blank interval was visible between the two grating presentations. This single grating-blank-grating sequence was employed to minimise any flicker adaptation resulting from the test stimulus presentation, since it is possible that the alternating presentation employed in previous experiments may produce some transient adaptation. Pilot work indicated that the single presentation yielded similar persistence measures to the alternating one.

Persistence was measured in blocks of trials, with the same adaptation stimulus being used throughout each trial block. An initial 90 sec adaptation period preceded each block. No persistence trial immediately followed this adaptation period, but after a short dark interval, a further 10 sec adaptation period was followed after 1 sec by a persistence

trial. Each subsequent persistence trial followed a 10 sec adaptation period and a 1 sec interval. The 1 sec interval between adaptation and test stimuli was kept dark to minimise possible loss of transient adaptation (Lovegrove, Mapperson & Bowling, 1980b).

The random staircase method described previously (Experiment 1) was employed, the duration of the ISI being changed in 10 msec steps. Each trial block continued until six threshold reversals had been obtained. Two blocks of trials were presented for each adaptation condition. The order of presentation of the adaptation conditions was counterbalanced across subjects, the second block of trials for each condition being in the reverse order to that of the first.

Results and Discussion

The mean persistence duration of the 2 c/deg grating was 200.2 msec after adaptation to the steady blank field. This was reduced to 174.2 msec following adaptation to the stationary grating, and to 170.5 msec after viewing the counterphase flickering grating. Adaptation to the stationary grating significantly reduced persistence duration ($t(5) = 3.54$, $P < 0.02$), as did adaptation to flicker ($t(5) = 3.94$, $P < 0.02$). There was no significant difference between the effects of flicker and stationary adaptation ($t(5) = 0.61$, $P > 0.05$). Adaptation to counterphase flickering and stationary 2 c/deg gratings consequently reduced persistence duration similarly.

The significant reduction in persistence duration after adaptation to stationary gratings supports the results of Meyer et al. (1975) and Meyer (1977), who used one long

adaptation period (approximately 15 min) and an alternating method of measuring persistence. The effects of flicker adaptation were, however, in the opposite direction to that anticipated. Adaptation to a counterphase flickering grating reduced, rather than increased persistence duration.

It is possible that both pattern and flicker detectors were adapted by the counterphase flickering grating producing the similar adaptation effects of both stationary and counterphase flickering gratings on persistence. Although the preliminary investigation showed that flicker adaptation selectively raised flicker threshold, some adaptation of pattern detectors may also have occurred. It is thus possible that use of a counterphase flickering grating confounds flicker and pattern adaptation effects. A subsidiary experiment in which pattern was eliminated by using a homogeneous blank flickering field as the adaptation stimulus was consequently performed. The same flicker frequency, test spatial frequency and presentation duration were used. Under these conditions the adaptation effects of flickering and steady blank fields on persistence duration were very similar (197.5 and 195 msec respectively).

These experiments have provided no evidence for the hypothesis that flicker adaptation increases persistence duration. It is possible, however, that the stimulus parameters employed were not adequate for substantial effects of adaptation upon persistence to be obtained. The flicker frequency may have been too high, as Petry et al. (1979) found that optimal flicker adaptation occurred at 7.7 Hz in their experiment. In addition, the brief (80 msec) grating presentation made

the persistence task a difficult one for subjects. The experimental procedure was consequently modified in the next adaptation experiment.

7.20 Experiment 12

In this experiment the adaptation stimulus was a blank field flickering at a frequency of 6.25 Hz . The test stimulus was a 1 c/deg sinusoidal grating presented for 400 msec.

A preliminary investigation of the effects of flicker adaptation upon detection threshold was performed with these stimulus conditions. Two subjects participated. The temporal modulation threshold for flicker detection was measured. Each subject adapted to the flickering stimulus for 90 sec, with the flicker detection threshold of the same stimulus being measured immediately afterward. Subjects were required to rotate a circular polarizing filter until they could just detect the flicker of an otherwise blank field. They took up to about 10 sec to make each threshold adjustment. Subsequent threshold measurements were made after 10 sec adaptation periods. With both subjects a pronounced decrease in threshold flicker sensitivity was observed after adaptation. The adaptation condition used in this experiment thus reduced flicker sensitivity and it was consequently assumed that transient mechanisms were being adapted.

Method

Subjects. These were fourteen graduate and undergraduate students of the Psychology Department. The majority had participated in previous experiments.

Apparatus. This was the same as for Experiment 11, except that an 0.6 contrast 1 c/deg grating was employed as the test stimulus.

Procedure. The procedure was similar to that described for Experiment 11. An initial 90 sec adaptation period preceded each trial block and a 10 sec adaptation period preceded each persistence trial. A dark 1 sec interval separated adaptation and test presentations. The 1 c/deg grating was presented for 400 msec, followed by the variable blank ISI and a further 400 msec presentation of the grating, and subjects were again required to indicate whether they saw the blank ISI.

There were two adaptation conditions, the steady blank field and the same field alternated with a dark interval at 6.25 Hz. Counterbalancing, block size and adaptation procedures were the same as in Experiment 11.

Results and Discussion

The mean persistence duration of the 1 c/deg grating was 145.1 msec after adaptation to the stationary field, and 150.1 msec after adaptation to the flickering field.

This difference was not significant ($t(13) = 1.27$, $P > 0.05$). There was a slight trend for persistence to be longer after adaptation to flicker than after adaptation to the stationary blank field, 11 of the 14 subjects giving small differences in this direction. Any increase in persistence duration following adaptation to flicker was so small, however, that, given the difficulty of the experimental task, it could not be discriminated from random variation.

After running 14 subjects, the difference was no closer to significance on a t-test than it was after 8.

General Discussion

The results of Experiment 11 indicate that there was no difference between stationary and counterphase flickering gratings in their adaptation effects upon persistence duration. Persistence was reduced by adaptation to a low frequency grating regardless of whether it was stationary or flickering. Experiment 12 also showed that there was no difference between steady and flickering fields in their adaptation effects. These results consequently provide no evidence that flicker adaptation increases persistence duration. The hypothesis that persistence is influenced by attempts to modify transient activity is not supported.

These results differ from those of Breitmeyer et al. (Note 2) who showed that the simultaneous presence of a flickering field increased the persistence duration of low spatial frequency gratings by 50-80 msec. A possible reason for this discrepancy is that flicker adaptation does not have as powerful an effect upon transient activity as the simultaneous presence of a flickering stimulus. There is some evidence that the effects of transient adaptation may rapidly dissipate (Lovegrove et al., 1980b). In these experiments, however, the total time required to present the persistence task after adaptation was no greater than 2 sec. Under similar adaptation conditions, subjects required much longer time periods to make threshold adjustments in the preliminary experiments. Substantial flicker adaptation was observed in these. The adaptation of transient mechanisms

should thus have lasted longer than the time taken to measure persistence.

Although transient mechanisms may take several seconds to fully regain their sensitivity, it is possible that considerable recovery occurs immediately after adaptation ceases. This possibility would explain the difference between the results of these experiments and those of Breitmeyer et al. (Note 2). Another possibility is that flicker adaptation affects the amplitude, but not the latency of transient mechanisms, and that off-response latency is the crucial variable determining persistence duration. As discussed previously, there is little evidence that flicker adaptation affects response latency (e.g. Kulikowski, 1977b). Alternatively, it is possible that transient off-responses do not have any effect at all on persistence duration. If this possibility proves to be the case, the results of Breitmeyer et al. (Note 2) may be explained by their methodology. The simultaneous presence of a flickering field with the persistence presentation may introduce complications into the already difficult persistence measurement task, for example, by changing subjects' criteria at low spatial frequencies.

It is concluded that the results of the experiments reported in this chapter offer no support for the hypothesis that transient off-responses terminate persistence. It is, however, possible that adaptation methods are not suitable for demonstrating this, or that the stimulus parameters used in the two experiments were not adequate to produce sufficent transient adaptation.

CHAPTER 8

ALTERNATIVE APPROACHES TO PERSISTENCE MEASUREMENT

The separation threshold method of measuring persistence has been used by a number of experimenters as well as by the present author. These include Haber and Standing (1969), Meyer (1977), Meyer et al. (1975), and, recently, Breitmeyer et al. (Note 2). There are, however, some problems associated with the use of this technique.

A major problem is one of criterion. All subjects in the persistence experiments reported in this thesis were given the same instructions; to indicate that they saw a blank interval only when a clear gap appeared between each grating cycle. They were instructed to ignore the presence of flicker. Different subjects, however, adopted widely differing criteria for the detection of the blank interval. It was apparent from the data that the differences between experimental conditions were often quite small when short ISI detection criteria were adopted. These differences were frequently much greater when the detection criterion was long. Subjects also experienced considerable difficulty in maintaining their criterion both within and between experimental sessions. It was frequently observed that criteria tended to lengthen during a session. These difficulties meant that the data were often quite variable.

One method of dealing with criterion problems has been to introduce catch trials (e.g. Lovegrove, Heddle & Slaghuis, 1980a). For a certain percentage of the trials, the blank ISI may be replaced with a grating similar in spatial frequency

and phase to the stimulus. The task then becomes a discrimination one, the dependent variable being the ISI at which the presentation containing the blank interval becomes discriminable from that with the grating. The rationale underlying this method is that persistence should make it impossible to identify the two conditions at short ISIs. Unfortunately, subjects may be able to base their judgements on cues other than the cessation of persistence. The apparent contrast of the presentation is less when the ISI is a blank field than when it is a grating, and this is especially true when brief stimulus durations are used. Subjects may make use of this difference in the apparent contrast of experimental and catch presentations to discriminate these. An experiment in which this method was used is described in this chapter.

The question also arises as to whether the separation threshold method always measures persistence. It has been shown that the presentation of a grating stimulus immediately after a brief flash of light will inhibit the detection of the light pulse (Campbell & Wurtz, 1978). This backward masking of a blank field by a grating is obviously unrelated to persistence. Forward masking may similarly occur. It is possible, therefore, that use of the separation threshold method of persistence measurement may be contaminated by these types of backward and forward masking. Furthermore, the response to one stimulus influences the response to a similar stimulus occurring some time afterwards (Phillips & Singer, 1974). The response to subsequent cycles of the stimulus in the separation threshold method may thus be

modified by the response to earlier ones, increasing or decreasing the persistence measure.

This chapter outlines a number of experiments designed to investigate the possible contribution of backward and forward masking to persistence measurements. Since a number of difficulties are associated with the separation threshold method, alternative methods of measuring persistence were also attempted. Pilot experimentation revealed that use of onset-offset adjustment methods of measuring persistence (e.g. Bowen et al., 1974; Haber & Standing, 1970) required highly practiced subjects, and they were, therefore, not practicable for the purposes of this thesis. The possible use of onset-offset reaction time methods was investigated.

8.10 Experiments 13-16

These experiments will be described jointly since they were performed simultaneously, using the same stimuli and subjects. The aim of the experiments was to investigate the extent to which a grating masked a blank field coming before or after it and the possible relationship between these effects and persistence. An experiment which attempted to measure the duration of integration between grating and blank was also included. If a blank field and a grating are both presented within the temporal integration period of the grating a composite percept combining the responses to the two stimuli should be produced. This percept should be similar whether the blank field comes before or after the grating. The composite percept would be expected to occur for longer blank durations with short grating presentations than with long ones. The duration of the blank field at which

the order of the two stimuli is identifiable should thus decrease with increasing stimulus duration. It was hypothesised that this decrease in the threshold blank field duration with increasing stimulus duration should asymptote at about the critical duration for each spatial frequency employed.

Method

Subjects. These were 8 University students recruited by means of the student employment service, and paid $2 per hour. Each subject completed five one hour experimental sessions, the first of which was a practice session on one of the experimental tasks.

Apparatus. Stimuli were photographic reproductions of sinusoidal gratings subtending 1, 4 and 8 c/deg when presented by means of a Gerbrands 4-field tachistoscope. The contrast of the gratings was approximately 0.6, and their luminance was maintained at 1.5 cd/m^2. Blank white cards were inserted into two tachistoscope fields and the luminance of one of these adjusted to 1.5 cd/m^2. This was the blank field which was presented either before or after one of the grating stimuli, or which occurred as an ISI between two presentations of the same stimulus. The luminance of the second blank field was kept very dim (< 1 cd/m^2). This field was illuminated continually except during the presentation of a stimulus. All fields were circular with a diameter of 5^o.

Procedure. In three of the four experiments the task involved the discrimination of trials containing the blank field from those in which the blank field was replaced by a grating similar in spatial frequency to the stimulus (catch trials). In the

fourth experiment, the order of the grating-blank sequence was the dependent variable. A blockwise tracking procedure (Lovegrove et al., 1980a) was used in each case with presentations commencing from slightly above or below approximate threshold as determined during preliminary testing. Blocks of 12 trials (6 test, 6 catch) were run, with the duration of the blank being increased or decreased by 10-20 msec between blocks. The blank field duration at which correct discriminations were obtained for 75% of the trials was taken as the detection threshold. Each of the 3 grating stimuli were presented for durations of 50, 100, 200 and 400 msec. The order of the spatial frequencies and durations was counterbalanced across subjects, all durations being run successively within each spatial frequency condition.

In Experiment 13 (backward masking) the blank field preceded the grating, and in Experiment 14 (forward masking) the blank field followed it. On fifty percent of the trials in each block the blank field was replaced by a grating for the same time period. Subjects were asked to identify the trials in which the blank field was present.

Experiment 15 involved a persistence measurement task of the type employed by Lovegrove et al. (1980a). Two equally long presentations of the same grating were separated by the variable duration blank field. For the catch trials, the blank was replaced with the grating for the duration of the ISI except for 30 msec immediately following the first stimulus. The blank field was presented for this 30 msec interval to introduce a slight flicker to the overall presentation. This was necessary to avoid the use of flicker as a

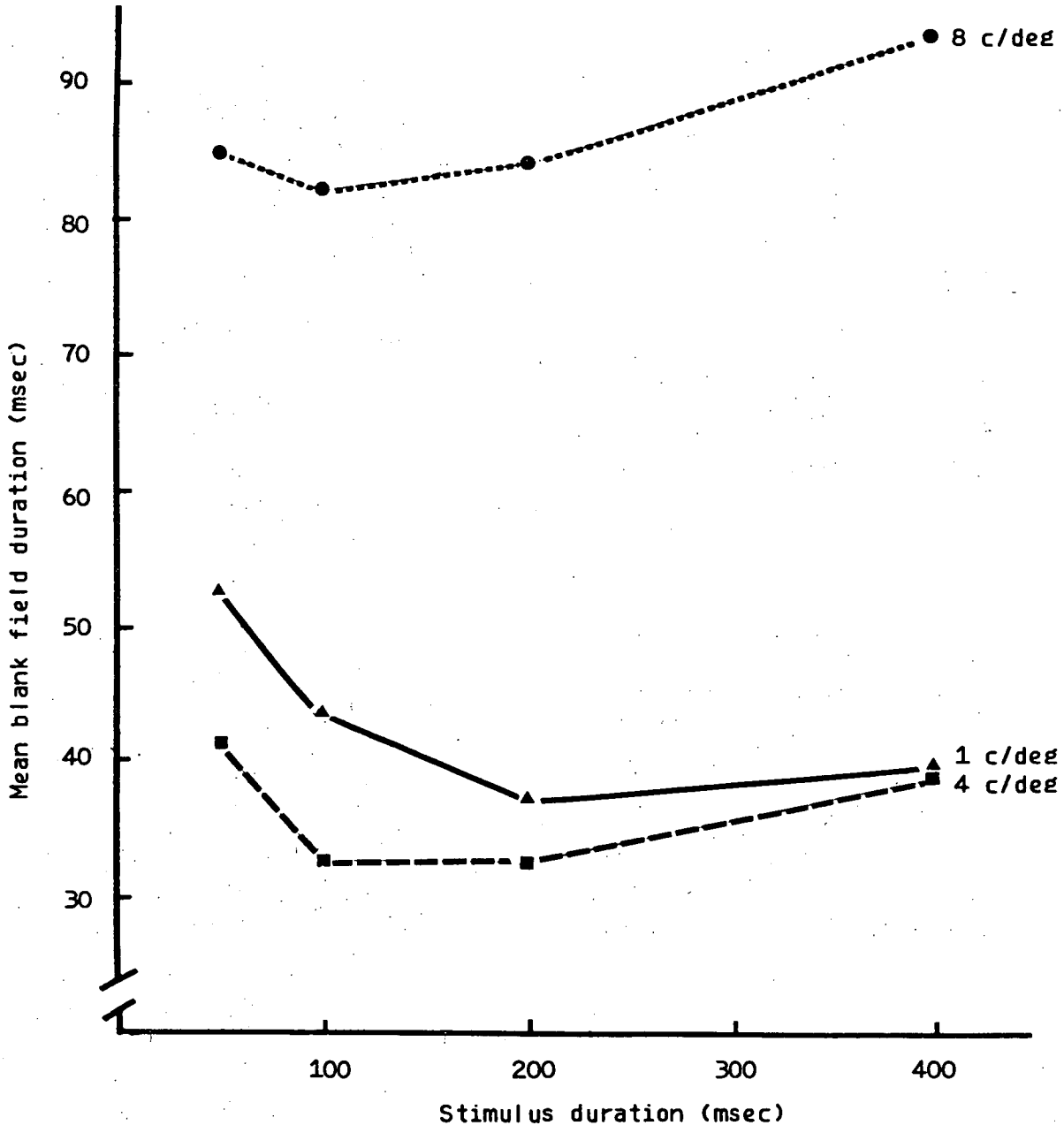

Figure 15. The mean detection threshold of a blank field preceding either a 1, 4 or 8 c/deg sinusoidal grating as a function of stimulus duration.

cue for discriminating between the two types of trial, as flicker was always present in the experimental trials. Subjects were again asked to identify the trials containing the blank ISI.

In Experiment 16, the blank field either preceded or followed the grating. The subject's task was to indicate the order of the two stimuli.

Results

8.11 Experiment 13

The mean threshold durations for detection of the blank field when it preceded the grating are shown in Figure 15. The figure indicates that backward masking of a blank field is dependent upon the spatial frequency of the grating, the 8 c/deg grating causing more prolonged masking than the 1 and 4 c/deg stimuli. This spatial frequency main effect was significant ($F(2,14) = 23.4$, $p < 0.001$). Although there was some variation in the degree of masking across stimulus durations, the duration effect was not significant ($F(3,21) = 1.64$, $p > 0.05$). The duration x spatial frequency interaction was also non-significant ($F(6,42) = 1.23$, $p > 0.05$). The backward masking duration was non-monotonically related to spatial frequency, the 4 c/deg grating producing shorter masking than either the 1 or 8 c/deg stimuli at every stimulus duration. The data from this experiment showed a considerable degree of consistency across durations and between subjects.

8.12 Experiment 14

These data were much less consistent than those of the

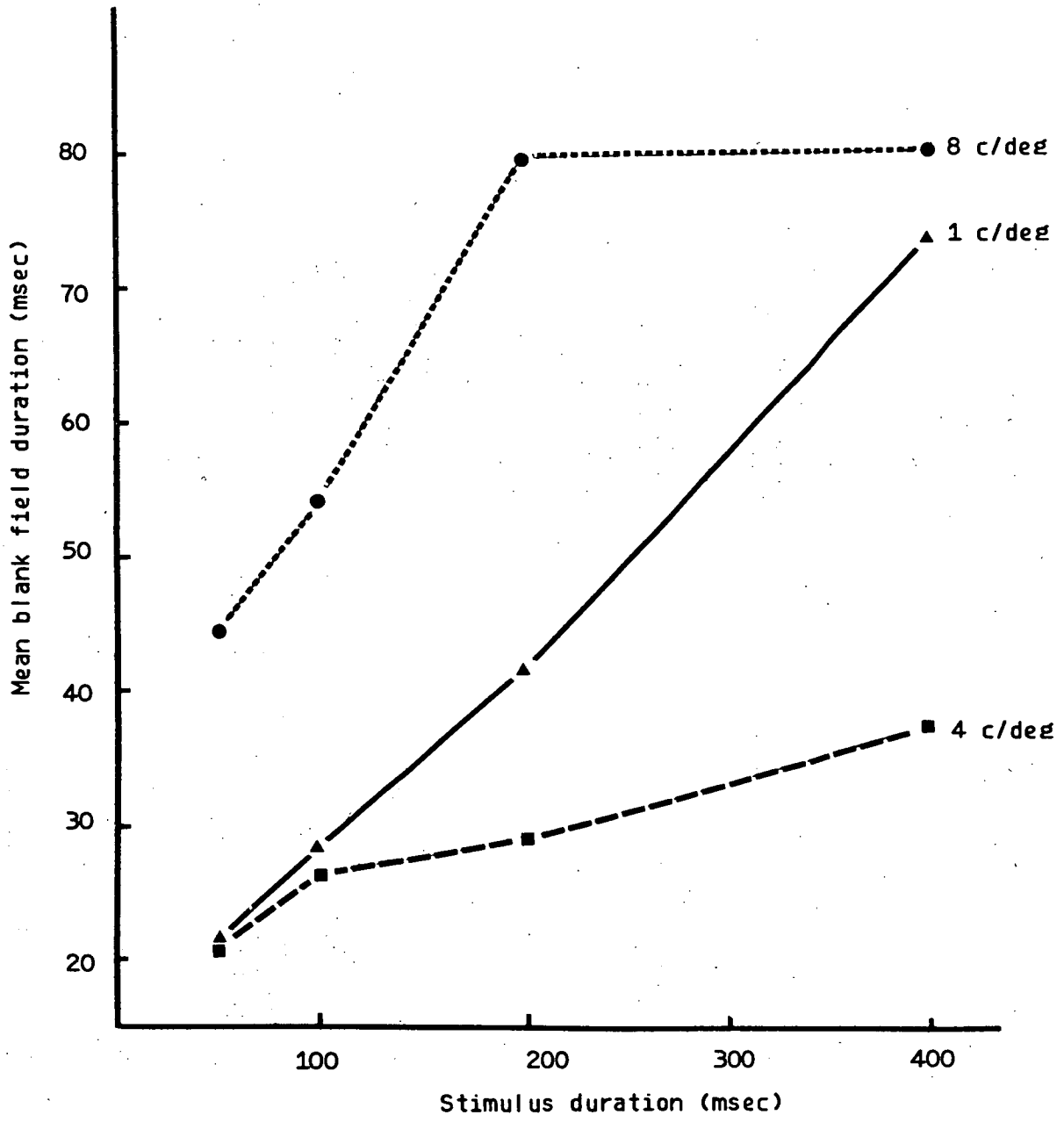

Figure 16. The mean detection threshold of a blank field following either a 1, 4 or 8 c/deg sinusoidal grating as a function of stimulus duration.

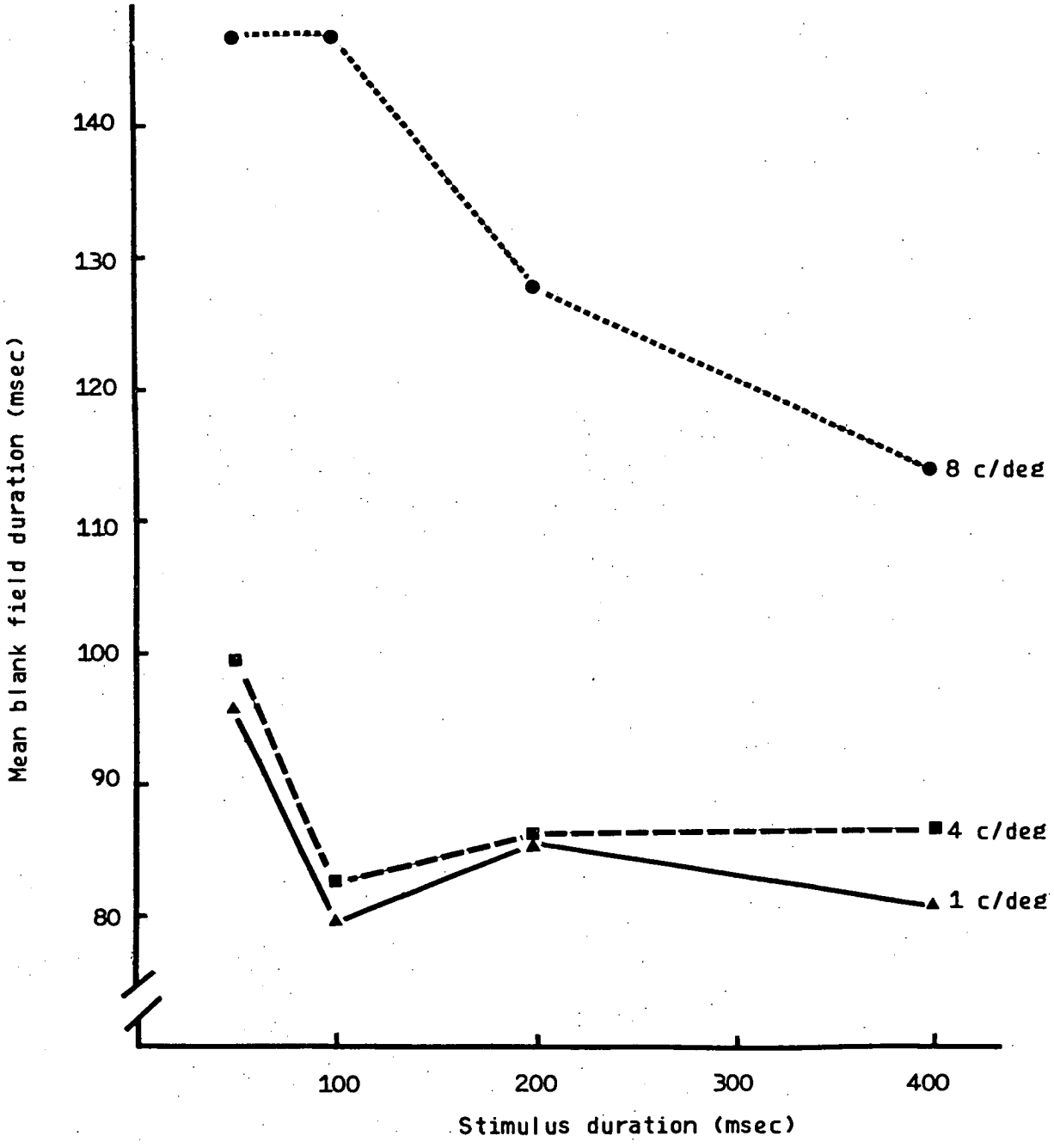

Figure 17. The mean detection threshold of a blank field occurring between two 1, 4 or 8 c/deg sinusoidal gratings (persistence) as a function of stimulus duration.

previous experiment, subjects showing marked variation in their ability to make the discriminations. The mean results are shown in Figure 16 as a function of stimulus duration. Again, a significant spatial frequency effect was obtained ($F(2,14) = 7.53$, $p < 0.01$), and the relationship between spatial frequency and masking duration was non-monotonic. In this experiment, however, the duration of forward masking increased significantly with increasing stimulus duration ($F(3,21) = 5.75$, $p < 0.01$). There was no significant spatial frequency x duration interaction ($F(6,42) = 1.32$, $p > 0.05$). The considerable increase in the 1 c/deg masking duration from the 200 to the 400 msec stimulus duration was due to one subject whose result for the 400 msec condition was exceptionally long.

8.13 Experiment 15

These data were again very variable, and because of significant inhomogeneity of variance a log transform was applied prior to analysis of variance. The mean detection thresholds of the blank ISI are shown in Figure 17 as a function of stimulus duration. As the figure indicates, the 8 c/deg data were much longer than those of the 1 and 4 c/deg stimuli. In contrast to the two previous experiments, the blank threshold duration increased monotonically with increasing spatial frequency. This spatial frequency effect was significant ($F(2,14) = 10.72$, $p < 0.01$), but there was no effect of duration ($F(3,21) = 1.91$, $p > 0.05$), or spatial frequency x duration interaction ($F(6,42) = 1.41$, $p > 0.05$).

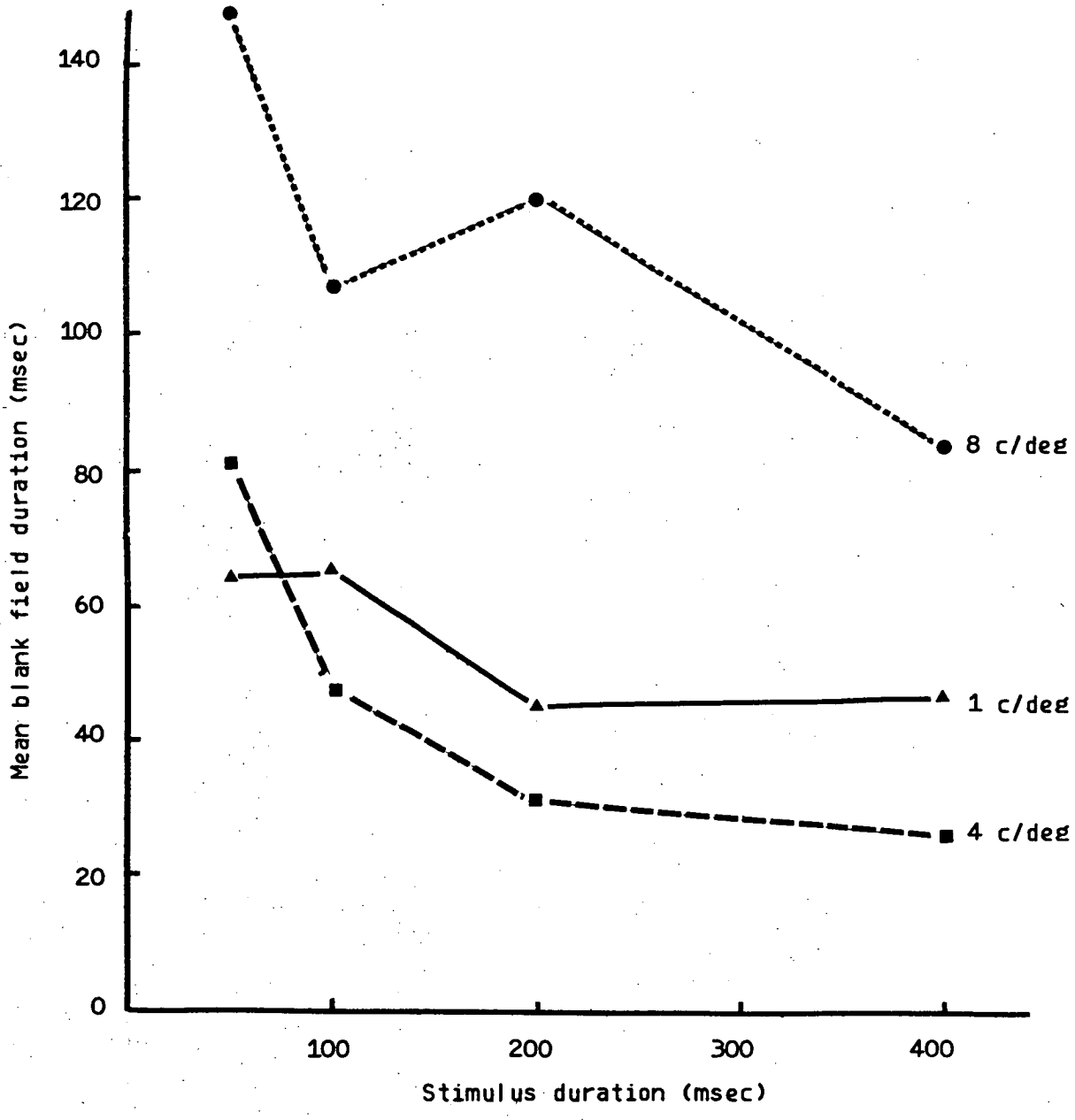

Figure 18. The mean duration of the blank field at which the order of presentation of the field and a 1, 4 or 8 c/deg grating is just identifiable.

8.14 Experiment 16

Again, considerable variability between individual scores made a log transformation of the raw data necessary. The mean blank durations at which the order of the grating-blank sequence was discriminable are shown in Figure 18 as a function of stimulus duration. The spatial frequency effect was highly significant ($F(2,14) = 28.61$, $p < 0.001$), and the threshold duration x spatial frequency relationship was non-monotonic except for the 50 msec stimulus duration where discrimination threshold increased monotonically with spatial frequency. The discrimination threshold decreased significantly with increasing stimulus duration ($F(3,21) = 4.18$, $p < 0.05$), but there was no spatial frequency x duration interaction ($F(6,42) = 0.50$, $p > 0.05$).

Discussion

A number of conclusions can be drawn from the four experiments described above, both singly and in combination.

1. Experiment 13 shows that, although the backward masking effect of a grating upon a blank field is dependent upon spatial frequency, it is not affected by stimulus duration. This result indicates that the inhibition of a blank field by a grating which follows it is unlikely to involve integration between the two stimuli. If the responses to the grating and the blank field were integrated by the visual system, a greater reduction in the apparent contrast of the presentation would be expected at short stimulus durations than at longer durations. The blank condition would then be most readily discriminated from the grating catch trials at the shortest stimulus duration, with threshold blank duration

increasing with increasing stimulus duration. Such an effect was observed in Experiment 14. Subjective observations also supported the conclusion that there was little integration between the blank field and the grating in the backward masking situation. The apparent contrast of the grating did not appear to be reduced by the presence of the blank field at any stimulus duration. The blank field was not detectable until its duration became long enough for it to be seen as a separate event occurring prior to the onset of the grating.

The backward masking effect may be caused by an inhibitory interaction between the pattern on-response and the response to the unpatterned blank field. Such a mechanism is unlikely, however, since the longer masking produced by the 8 c/deg grating would mean that this stimulus produces the most powerful on-response. All the literature on transient on-responses indicates that they decrease in magnitude and increase in latency with increasing spatial frequency (e.g. Breitmeyer, 1975a). In addition, the masking duration x spatial frequency relationship is non-monotonic, and appears to mirror the contrast sensitivity function, a result which would not be expected from an on-response inhibition hypothesis. A similar relationship between backward masking duration and spatial frequency was obtained by Potter (1979). The shape of this relationship may indicate that the apparent contrast of the stimulus determines masking duration. Further experimental work is necessary to investigate this possibility.

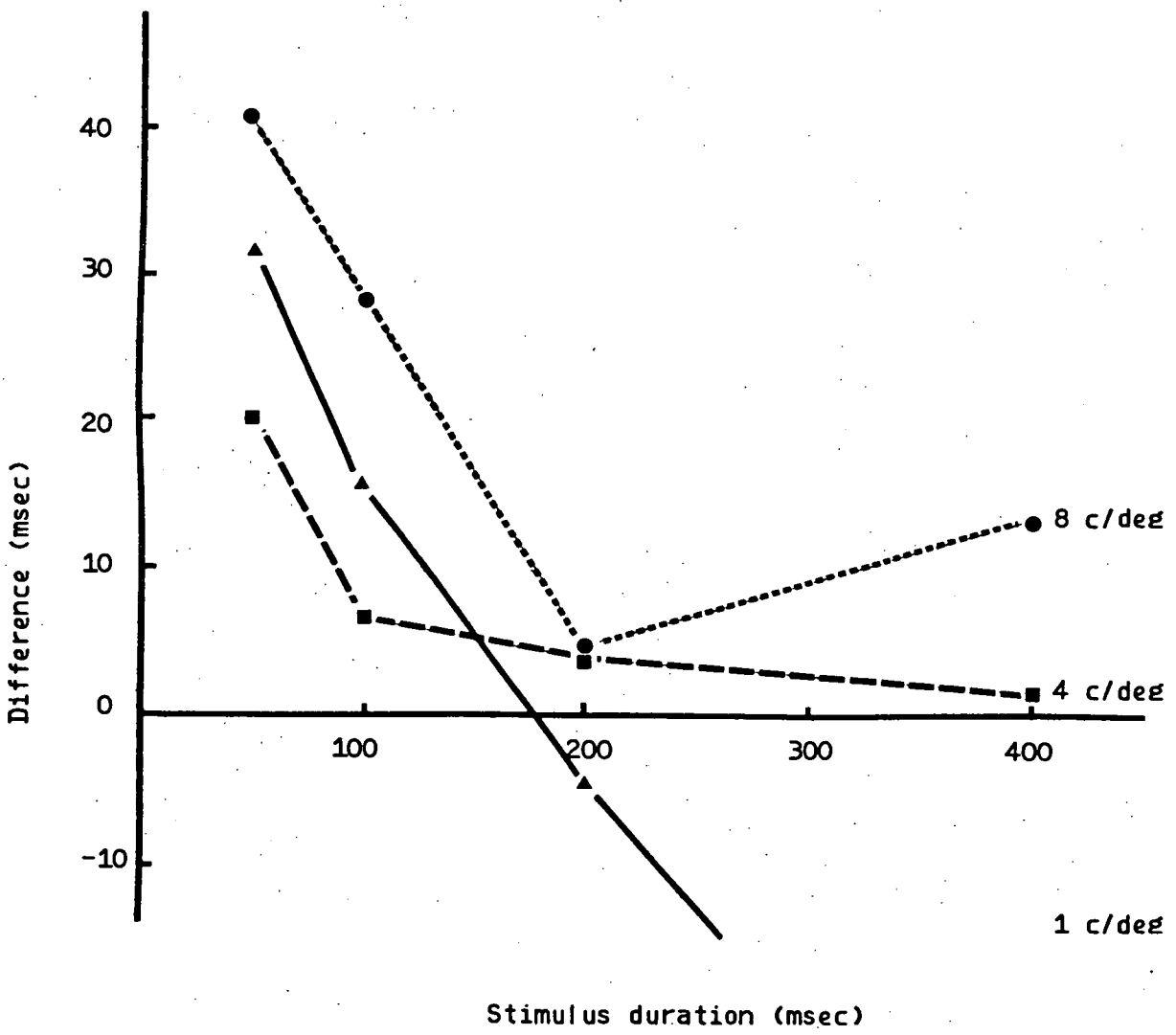

Figure 19. Graph showing the difference between the mean blank field durations for backward (Experiment 13) and forward masking (Experiment 14) situations.

2. The data from Experiment 14 show that, in the forward masking condition, the blank detection threshold is quite brief at the 50 msec stimulus duration, but increases to approximately the same duration as observed in the backward masking experiment at 400 msec. (The 1 c/deg 400 msec condition is, however, somewhat anomalous in this respect). It is possible that two mechanisms may influence the discrimination task in the forward masking situation - integration at short durations and some form of inhibition (as for the backward masking situation) at long stimulus durations. Figure 19 shows a plot of the difference between the mean results of the backward and forward masking experiments. This difference tends to asymptote to zero for the 4 and 8 c/deg data. The stimulus duration at which the difference approaches zero is approximately 100 msec at 4 c/deg, and 200 msec at 8 c/deg. These stimulus durations may reflect the different integration times of the two stimuli. This observation strengthens the hypothesis that in the forward masking situation, integration between grating and blank field reduces the apparent contrast of the total percept. This reduction in apparent contrast facilitates the detection of the presence of the blank at short stimulus durations. With longer stimulus durations, however, no contrast reduction would be expected, and at these durations, the mechanism which inhibits the detection of the blank field should be similar to that which occurs in the backward masking paradigm. It is consequently proposed that in the forward masking condition the inhibitory mechanism operates similarly at all stimulus durations, but at short stimulus durations, the reduction in the apparent contrast of the presentation facilitates the discrimination between the experimental and catch trials.

The inhibition mechanism may be related to the 'grey-out' inhibition observed during saccadic eye movements (Campbell & Wurtz, 1978).

3. A comparison of the results of Experiments 13 and 14 with those of Experiment 15 reveals a number of differences between the masking and persistence paradigms. These differences indicate that the detection threshold of a blank field occurring between two gratings is not merely the sum of forward and backward masking components. The most noticable difference between the two paradigms is that, whereas the blank detection threshold is non-monotonically related to spatial frequency in both masking experiments, it is a monotonic increasing function of spatial frequency in Experiment 15. This relationship is similar to that served in other persistence studies (e.g. Lovegrove et al., 1980, Meyer & Maguire, 1977). In addition, the sum of the masking durations from Experiments 13 and 14 increases with increasing stimulus duration, but the ISI in Experiment 15 decreases slightly with increasing duration. It may therefore be concluded that the method employed in Experiment 15 does not measure the total duration of backward and forward masking of the blank ISI by the two grating presentations. In the light of the considerable differences between the results of the masking and persistence paradigms, it is unlikely that forward and backward masking contaminates the persistence results to any extent.

The method of persistence measurement employed in Experiment 15 did not produce the previously observed decline in persistence with increasing stimulus duration (Experiments 5, 7, 8

and 9), especially with the 1 and 4 c/deg stimuli. This agrees with the results of an experiment by Badcock (1979) in which a similar method was used to measure persistence over two stimulus durations. The major difference between the experimental method described here and the separation threshold method is the presence of catch trials in the current experiment (although a difference in the number of cycles of the stimulus presentation also occurred). As described in the introduction to this chapter, a reduction in the apparent contrast of the grating-blank-grating presentation may have made it more readily discriminable from the catch trials at short stimulus durations. This would produce shorter apparent persistence durations than anticipated at these stimulus durations.

4. A non-monotonic relationship between spatial frequency and the threshold blank field duration for discrimination of the order of the stimuli was obtained in Experiment 16. This relationship was similar to that obtained in the masking experiments, and indicates that processes similar to those occurring in the masking experiments operated here. Although the threshold blank field duration declined with increasing stimulus duration, the time period over which the responses to grating and blank were integrated by the visual system could not be determined from this relationship. The longer blank field durations required for correct order discriminations at short stimulus durations may have been partly due to integration processes as described earlier. Additional processes affecting order discrimination may have been operating at shorter stimulus durations, however, as Experiments 13 and 14 have shown that the discrimination of the

presence of the blank field may be based on different processes in the forward and backward masking situations. At the 400 msec duration the same processes apparently operate in both forward and backward masking conditions and here the blank field durations required for order discrimination were very similar to the masking durations. At this stimulus duration, the order of the stimuli is consequently discriminable only when the duration of the blank field is long enough for it to evade masking.

5. It may be concluded from the results of Experiments 13 and 14 that the measurement of persistence Component 2 is unlikely to be contaminated by forward or backward masking in the separation threshold method, as was suggested in chapter 6. Persistence always increases monotonically wit spatial frequency at long stimulus durations (Experiments 5 and 6), but the duration of both backward and forward masking is non-monotonically related to spatial frequency. If the duration of backward masking contributed substantially to the measurement of persistence, a 4 c/deg grating would have shorter 'persistence' than the 1 c/deg grating at these durations. Figure 7 shows that this is not the case.

8.20 Reaction time experiments

This section reports the results of experiments in which the offset and onset reaction times to gratings were obtained under various experimental conditions. The difference between these reaction times has been considered to be a measure of persistence (e.g. Briggs & Kinsbourne, 1972; Erwin & Hershenson, 1974). The results of these experiments, however, indicate that the reaction time difference does not measure

the same phenomenon as the persistence paradigm described in previous chapters. The dependent variable in these experiments will consequently be called the 'offset-onset reaction time difference'.

8.21 Experiment 17

This experiment was an attempt to replicate the results of Experiment 5 using the reaction time method. Onset and offset reaction times to 2 and 8 c/deg gratings were obtained for stimulus durations ranging from 40-500 msec.

Method

Subjects. These were eight undergraduate Psychology students. Seven of these had participated previously in a similar reaction time experiment, and in a contrast threshold experiment where similar spatial frequencies and stimulus durations were employed.

Apparatus. Vertical sinusoidal gratings were generated on a b.w.d. oscilloscope screen. The relative contrast of the stimuli (in volts) was measured by means of a multimeter attached to the oscilloscope function generator. Contrast threshold for each stimulus condition was previously obtained for eight subjects and averaged. The contrast level of each stimulus condition was set at 25x this average threshold value so that the apparent contrast of all stimuli was approximately the same. The luminance of the oscilloscope screen was held constant at 2.2 cd/m^2. Reaction time was measured by means of an electronic timer which was activated by the onset of the grating presentation, and terminated by a reaction time switch held in the subject's

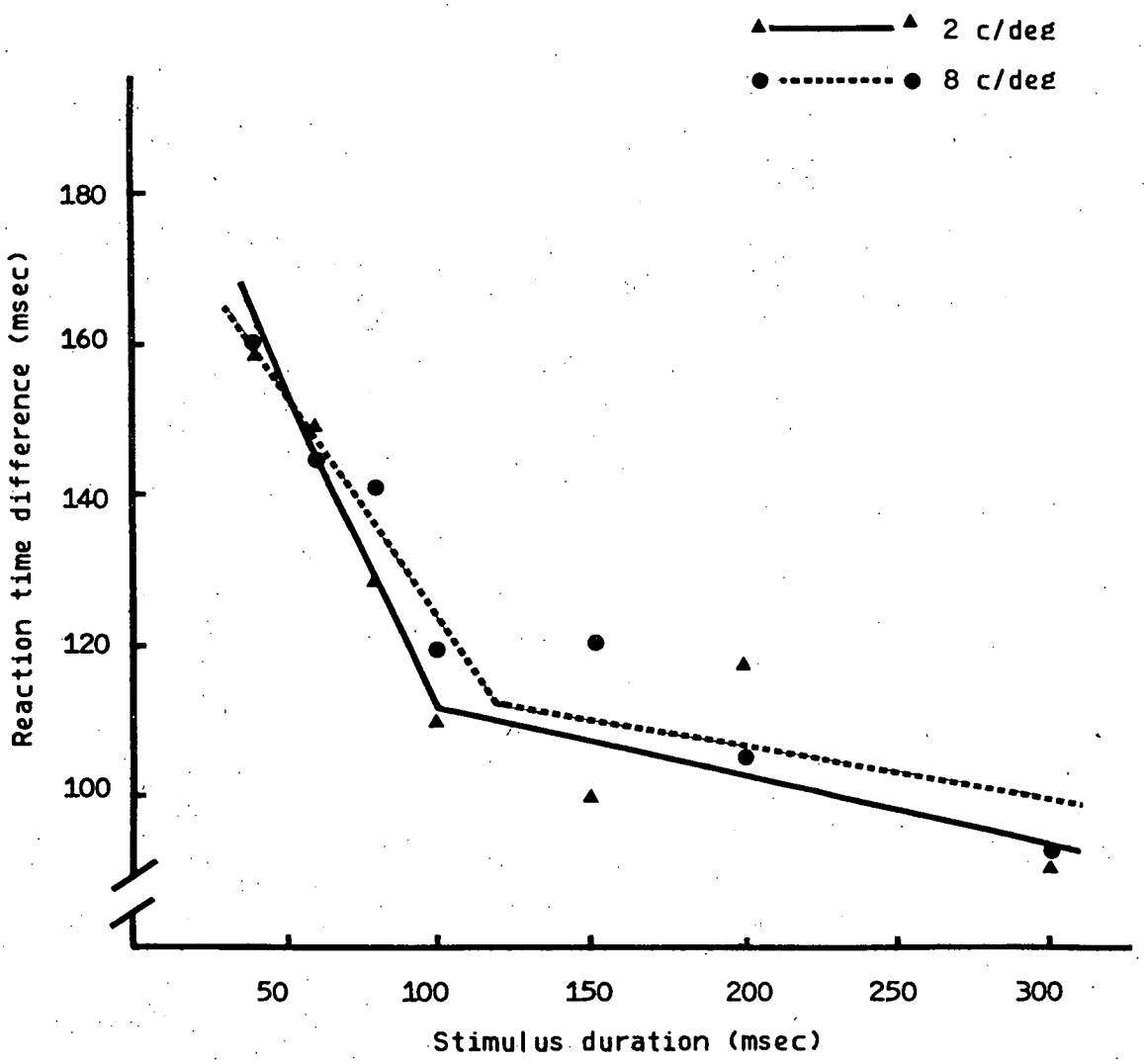

Figure 20. Mean difference between offset and onset reaction times to 2 and 8 c/deg gratings as a function of stimulus duration.

dominant hand.

Procedure. Subjects viewed the occluded 2^{o} circular oscilloscope screen from a distance of 228 cm. After a variable foreperiod, the grating appeared on the oscilloscope screen for the specified duration following initiation by the subjects, who then responded to either the onset or the offset of the grating by pressing the reaction time switch. For the offset reaction time trials subjects were instructed to respond to the reappearance of the blank screen following the grating. Practice reaction time trials were given for at least 5 min preceding the collection of data. Reaction times were obtained for 40, 60, 80, 100, 150, 200 and 300 msec presentations of both the 2 and 8 c/deg gratings, and at 500 msec for the 8 c/deg stimulus. Ten onset and fifteen offset reaction times were obtained in groups of 5 for each condition. The stimulus durations were presented in a random order, and the order of the spatial frequencies and onset and offset reaction time conditions was counterbalanced across subjects.

Results and Discussion

The mean offset-onset reaction time difference for each spatial frequency is depicted as a function of stimulus duration in Figure 20. This difference declined with increasing stimulus duration for both spatial frequencies. An analysis of variance (excluding the 8 c/deg 500 msec condition) showed that this main effect of duration was highly significant ($F\ (6,42) = 9.95$, $p < 0.001$). There was no significant spatial frequency effect ($F\ (1,7) = 1.42$, $p > 0.05$), nor spatial frequency x duration interaction

($F(6,42) = 1.15$, $p > 0.05$). Figure 20 indicates that there was very little difference between the two spatial frequencies at any stimulus duration. This is at variance with the persistence data of Experiment 5. The offset-onset reaction time difference therefore measures a phenomenon other than persistence.

Two intersecting straight lines could be fitted to the reaction time difference x duration relationship in the same manner as for Experiment 5. The initial slopes of these lines were -0.83 for the 2 c/deg data and -0.61 for the 8 c/deg data. The intersection durations were 100 and 120 msec respectively. The difference between offset and onset reaction times consequently declined with a slope approaching -1.0 with increasing stimulus duration up to about 100 msec for both spatial frequencies. After 100 msec the slope of the relationship became less steep. Assuming that the onset and offset reaction times measure the latencies of transient on- and off-response respectively (e.g. Coltheart, 1980), this initial slope indicates that off-response latency is dependent upon on-response latency at short stimulus durations (less than 100 msec). That is, the off-response occurs a relatively fixed amount of time after the on-response. (This interval increases somewhat with increasing stimulus duration, producing a slope less than -1.0). Using the VEP, a similar relationship between on- and off-response latency has been observed by Serviere et al. (1979). The failure to find any large difference in the intersection durations between the two spatial frequencies indicates that this interval between on- and off-responses is inde-

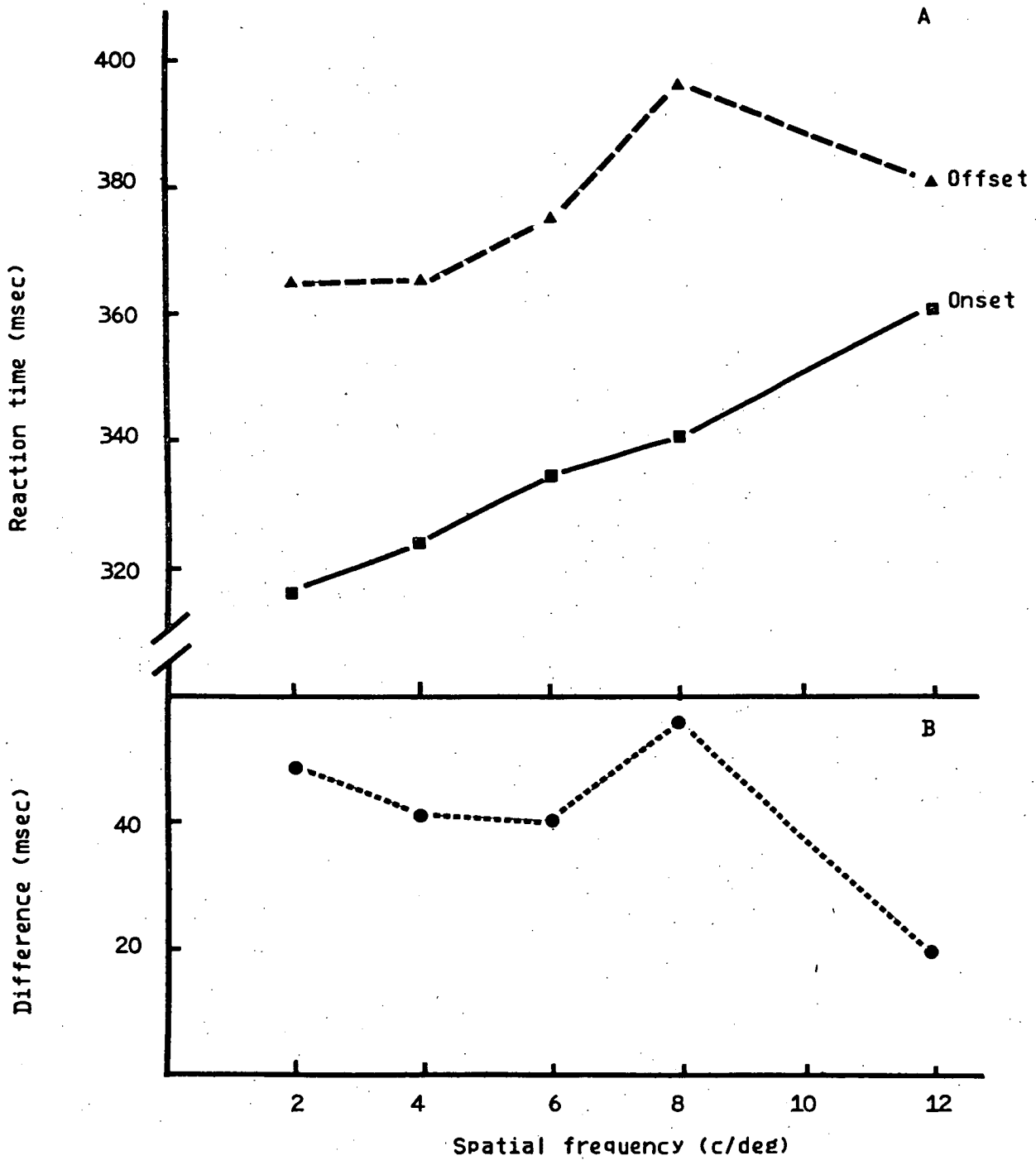

Figure 21. (A) Mean onset and offset reaction times to gratings as a function of spatial frequency.

(B) Offset - onset reaction time difference as a function of spatial frequency.

pendent of spatial frequency.

The results of this experiment indicate that, although both off- and on-response latency increases with increasing spatial frequency (Breitmeyer, 1975a; Breitmeyer et al., Note 2), this does not affect the difference between them. The failure to obtain any effect of spatial frequency on the offset-onset reaction time difference was investigated further in the next experiment.

8.22 Experiment 18

In this experiment onset and offset reaction times to gratings were determined as a function of spatial frequency using a stimulus duration of 100 msec.

Method

The method was similar to that of Experiment 17 with six undergraduates serving as subjects. Twenty-five onset and offset reaction times to 2, 4, 6, 8 and 12 c/deg sinusoidal gratings were obtained, with the spatial frequency on any trial being randomly selected. Twenty-five percent catch trials were included for both onset and offset conditions. For onset reaction time the catch trial was a brief change in luminance instead of a grating stimulus. For offset reaction time it was a 500 msec presentation of the stimulus.

Results and Discussion

The onset and offset reaction times together with the difference between them are shown as a function of spatial frequency in Figure 21. Onset reaction time increased significantly with increasing spatial frequency ($F(4,20) = 7.62$, $p < 0.001$), as did offset reaction time ($F(4,20) = 5.11$,

$p < 0.01$). There was no significant effect of spatial frequency on the offset-onset reaction time difference ($F(4,20) = 2.12$, $p > 0.05$). This result confirms the previous observation that there is no effect of spatial frequency on the difference between onset and offset reaction times (also Breitmeyer et al., Note 2).

The possibility that the reaction time method measures the subject's reaction to fast latency transient on- and off-responses has been considered in chapter 2. In the current experiment, any reaction to transient on-responses should have been avoided by the presence of flicker catch trials. It was necessary for subjects to clearly perceive pattern before responding, and it is therefore likely that onset reaction time was determined by pattern detecting (sustained) mechanisms. In the offset condition, however, an off-response presumably always accompanied termination of the stimulus. Offset reaction time may consequently have been determined by the transient off-response latency, rather than by the end of the pattern percept.

A possible means of measuring pattern persistence using an offset-onset reaction time method may be to dissociate pattern termination and off-responses. This may be done by including catch trials in which a low contrast grating follows the test grating. Only presentations in which the grating is followed by a clear blank field are regarded as experimental trials. In this case, an off-response does not always signal pattern termination and subjects must respond to the disappearance of pattern, rather than to the offset of the high contrast grating.

8.23 Experiment 19

In this experiment the offset-onset reaction time difference was again measured as a function of spatial frequency, with offset catch trials as described above being included.

Method

Stimuli were photographic reproductions of sinusoidal gratings presented by means of a Gerbrands 4-field tachistoscope at a luminance of 1.5 cd/m^2. The field was circular, subtending a visual angle of 3^o. Eight undergraduates participated as subjects.

Twenty four onset and offset reaction times to 50 msec presentations of 1, 2, 4 and 8 c/deg gratings were obtained in blocks of 12. Twenty-five percent of both onset and offset reaction time trials were catch trials, the onset catch trial being a brief change in luminance as in Experiment 18. In the offset catch trials the test grating was followed by a low contrast grating of the same spatial frequency for 1 sec. Subjects were told to respond only to the absence of pattern.

Results and Discussion

The mean results for the offset-onset reaction time difference are given in Table V. The difference increased by 25 msec from 1 to 8 c/deg, but this was not significant ($(3,21) = 0.50$, $p > 0.05$). The use of a pattern criterion for both onset and offset reaction time conditions consequently did not produce a significant spatial frequency dependent increase in the offset-onset reaction time difference.

TABLE V.

Mean onset and offset reaction times to gratings followed by a low contrast grating of the same spatial frequency and the offset - onset reaction time difference.

SPATIAL FREQUENCY (c/deg)	REACTION TIME (msec) ONSET	OFFSET	DIFFERENCE
1	295	475	180
2	292	475	183
4	295	495	200
8	302	505	203

The dependent variable of Experiment 19 is consequently unrelated to persistence as measured in Experiments 1, 5 and 6.

Is is possible that after-images had a confounding effect in this experiment especially at low spatial frequencies. It was not always possible to make a rapid discrimination between experimental and catch trials because after-images frequently followed the experimental trials. Artificially long offset reaction times may consequently have been obtained at low spatial frequencies.

Discussion of Reaction Time Experiments

The results of these experiments indicate that onset-offset reaction time methods do not measure the same phenomenon as the separation threshold method employed in Experiments 1-9. It is probable that short-latency transient on- and off-responses were primarily responsible for the reaction times, but where catch trials were employed, as in Experiments 18 and 19, sustained mechanisms may also have been involved to some extent.

Two points relevant to the theoretical aspects of this thesis emerge from these experiments:

(1) The lack of any effect of spatial frequency on the offset-onset reaction time difference indicates that the hypothesis that persistence duration is affected by off-response latency may not be correct. If transient off-responses terminate persistence as was suggested in chapter 4, increasingly longer off- than on-response latency would be expected with increasing spatial frequency. The lack of any

spatial frequency related reaction time difference is therefore consistent with the failure to find any effects of flicker adaptation on persistence described in chapter 7. Transient off-response latency possibly has no relationship to separation threshold measures of persistence.

(2) Experiment 17 indicates that off-response latency is dependent upon on-response latency at short stimulus durations, and that the duration of the interval between on- and off-response is independent of spatial frequency. This suggests that integration time is not determined by the interval between on- and off-responses, as was suggested by Efron (1973), since critical duration increases with increasing spatial frequency (e.g. Legge, 1978).

CHAPTER 9

SUMMARY AND CONCLUSIONS

The experiments reported in this thesis have shown that separation threshold measures of persistence depend upon the spatial frequency, orientation and contrast of grating stimuli, and upon the duration of the stimulus presentation. The effect on persistence duration of each of these parameters has been related to other spatio-temporal properties of the visual system. It was proposed that visible persistence results from the lack of fine temporal resolution at both peripheral and central levels of the visual system. The results of the experiments and the conclusions derived from them are summarised below.

1) The duration of visible persistence was found to increase linearly with spatial frequency, confirming the results of Meyer and Maguire (1977). The similarity between this relationship and the spatial frequency dependent increase in critical duration observed by Legge (1978) suggested that both critical duration and persistence were due to similar underlying neural processes. The critical durations of transient mechanisms appear to be shorter than those of sustained mechanisms (Breitmeyer & Ganz, 1977; Legge, 1978), and it is possible that the increase in persistence is due to a gradual changeover from transient to sustained activity with increasing spatial frequency. Alternatively, the response durations of

sustained mechanisms alone may increase with spatial frequency (Breitmeyer & Ganz, 1976), giving rise to the observed relationship between persistence and spatial frequency. The latter hypothesis appears to be more likely with separation threshold measures of persistence duration. With this method, the continuation of pattern is the criterion for assessing persistence duration, with the appearance of flicker (transient activity) being ignored. It was also proposed that transient off-responses may influence the relationship between persistence and spatial frequency by inhibiting sustained responses at low spatial frequencies. The reaction time studies, however, indicated that this is unlikely since no spatial frequency dependent increase in the difference between on- and off-response latency was observed. It was consequently concluded that sustained mechanisms responsive to high spatial frequencies have longer response times than those activated by lower spatial frequencies, causing an increase in persistence duration with increasing frequency.

2) Persistence duration decreased logarithmically with increasing contrast. This logarithmic relationship showed some similarity to the relationship between contrast and response amplitude in cat cortical neurones (Maffei, 1978), and to that between contrast and various components of the human VEP (Kulikowski, 1977a). There was also considerable similarity between the decrease in persistence (possibly transient activity) with increasing contrast and the logarithmic decrease in the response latency of early components of the VEP with contrast (Kulikowski, 1977a). Kulikowski's results and the reaction time data of Harwerth and Levi (1978)

indicate that transient activity becomes increasingly pronounced at high contrast levels. These observations led to the conclusion that the reduction in persistence duration with increasing contrast may be due to an increase in the amplitude or a decrease in the latency of transient off-responses.

Neither the adaptation nor the reaction time experiments, however, provided any evidence that transient activity affects persistence duration. The proposal that reduced contrast increases persistence by decreasing transient activity was consequently not supported. An alternative explanation is that a low contrast stimulus may give rise to a longer sustained response than a high contrast stimulus. A general trend for persistence to be longer for weak than for intense stimuli has been observed. Longer persistence also occurs at high spatial frequencies, oblique orientations, low luminance levels and when the stimulus presentation is made to the non-dominant eye (Harris, Note 3). In addition, informal observations indicate that persistence is longer when a stimulus is presented in the orientation where astigmatic subjects have reduced acuity. The contrast effect may consequently be a specific instance of this tendency for the responses to weaker stimuli to be prolonged. Further work is necessary to investigate the mechanisms which prolong persistence under these conditions.

3) The persistence of oblique gratings was longer than that of vertical or horizontal ones, indicating that persistence duration is influenced by cortical mechanisms. This orientation effect may be due to similar processes to those

prolonging the persistence duration of low contrast stimuli. The failure to obtain any evidence that transient off-responses may be responsible for the contrast effect means that the proposal presented in chapter 6 that two separate mechanisms are responsible for the two effects is no longer necessary.

4) There was no difference in persistence duration between square and sine wave gratings. This presumably indicates that persistence is determined by the low frequency components of a stimulus.

5) With brief stimuli, persistence duration was inversely related to stimulus duration. At longer durations, the persistence x duration relationship was relatively flat. On the basis of this relationship, two persistence components were proposed to contribute to the total persistence duration. The first of these was considered to be due to integration processes at the peripheral level of the visual system, since the stimulus durations at the change in the slope of the relationship were similar to threshold measures of critical duration. The total duration of the peripheral neural response to a brief stimulus was considered to be relatively independent of stimulus duration, so that persistence declined linearly with a slope approaching -1.0 as stimulus duration increased.

6) It was demonstrated that orientation did not affect the first persistence component but that the duration of the second component was longer with oblique than with vertical gratings. It was inferred that the second persistence component results from activity in cortical sustained mechanisms.

7) The contrast effect predominated in the second persistence component and thus appeared to result from cortical processes.

8) Although flicker adaptation did not increase persistence duration, adaptation to stationary and flickering pattern decreased persistence duration equally. The results of the reaction time experiments also indicated that persistence duration may not be influenced by off-responses latency, as was originally proposed in chapter 4.

The results of the experiments support the two-component theory of persistence described in chapter 2, although some modifications are necessary. The initial slope of the persistence x duration relationship was not -1.0 as would be expected if temporal integration was perfect. In addition, the secondary slope of the relationship was slightly less than zero. The discrepancies between these data and the results of Efron (1970a) may be due to differences between the integration properties of patterned stimuli and spots of light. Although perfect duration x intensity reciprocity is observed at threshold with small homogeneous light spots, time x contrast reciprocity is not perfect with grating stimuli (e.g. Breitmeyer & Ganz, 1977). The initial slope of -0.70 observed by Breitmeyer and Ganz for the log contrast x log duration relationship at threshold is very similar to the overall initial slope of -0.69 obtained for the 4 c/deg persistence x duration relationship. The shallow slope may indicate that the duration of the neural response is not altogether independent of stimulus duration, but that it increases slightly with increasing duration.

The finding that the secondary slope of the relationship is not zero means that the duration of the second persistence component is also influenced to some extent by the duration of the stimulus. Stimulus duration had its greatest effect on the duration of this component at low contrast levels. The fact that the duration of the second persistence component was not constant and that the initial slope was not -1.0 means that the relationship between stimulus duration (t), critical duration (C), and peripheral and central persistence (P_C) described in equation (2) in chapter 2 must be modified slightly. The relationship now becomes

$$P = C - 0.70t + P_C - at \qquad t < C$$

$$P = P_C - at \qquad t > C \quad \ldots\ldots\ldots \quad (4)$$

where P_C is obtained from the y-intercept of the secondary component of the relationship, and a is the slope of this component. The value of a is approximately -0.1, but this may vary with contrast level (see Table III). The values of C and P_C are dependent upon the spatial frequency of the stimulus.

It was hypothesised that the second persistence component may be a result of cortical sustained cell activity. The possibilities that it could be an artifact of subjects' criterion, or that it may be due to forward and backward masking of the blank ISI by the grating were eliminated. A further possibility requiring investigation is that successive grating cycles of the alternating presentation may interact to produce an elevation in apparent persistence. Such a mechanism is plausible, since the existence of the second component is only demonstrable when techniques requiring two or more successive presentations of similar stimuli are employed to measure

persistence (Coltheart, 1980). This applies to the separation threshold method used for Experiments 1-9. In these experiments, however, mutual inhibition between on- and off-responses (e.g. Phillips & Singer, 1974) is unlikely to increase persistence duration since the separation technique is not likely to involve judgements based on transient activity. The stimulus presentation is seen to be flickering at much shorter ISIs than those at which a clear break in the pattern percept occurs. Although the transient on- and off-responses are readily perceived, they are consequently unlikely to affect the duration of the pattern percept. Methods which do not obtain any persistence at long stimulus durations may be more dependent upon off-responses than the separation threshold method of measuring persistence. The use of the onset-offset adjustment method to investigate the effects of spatial frequency, contrast and duration upon persistence may provide more information about the role of off-responses under these conditions.

The results of Experiment 8 provide evidence that contrast affects persistence at the cortical, rather than at the peripheral level. Luminance probably affects persistence at the peripheral level. It is therefore likely that the mechanism by which contrast affects persistence is different than that by which persistence is affected by luminance. It is hypothesised that decreased luminance may increase persistence by increasing the response duration of transient retinal ganglion cells by causing them to behave in a more sustained fashion (e.g. Jakiela et al., 1976). Further

studies of the relationship between luminance and persistence are necessary to test the hypothesis that the luminance effect is peripheral. The hypothesis predicts that decreased luminance would only affect the duration of the first component. This may be investigated by measuring persistence duration at two luminance levels across several stimulus durations. Since the duration of temporal integration increases with decreasing luminance, the maximum duration of Component 1 would be expected to increase similarly. If luminance only affects peripheral processes, the persistence durations of stimuli longer than the critical duration should not be affected. Such a result would establish the location of the luminance effect and provide further evidence for the identification of Component 1 with temporal integration.

Experiments 5, 7, 8 and 9 have shown that persistence duration decreases with increasing stimulus duration, and Experiments 1, 2 and 8 have also shown that it increases with decreasing contrast. It could consequently be argued that the duration effect is due to the reduction in the apparent contrast of brief stimuli rather than to stimulus duration itself. To eliminate this possibility it would be necessary to run an experiment which investigated the effect of duration on the persistence of stimuli of equivalent apparent contrast. If Component 1 is a manifestation of temporal integration, stimulus duration would be expected to have a similar effect on persistence under these conditions as under the conditions of Experiments 5, 7, 8 and 9. Using the onset-offset adjustment method, Bowen et al. (1974) have run an experiment in which the apparent brightness of light flashes was equated across stimulus durations by using equal energy stimuli. No duration effect was observed at

short stimulus durations in this experiment. This finding requires further investigation, since temporal integration methods of measuring persistence duration normally yield an inverse relationship between persistence and duration with equal energy stimuli (Di Lollo, 1977; Di Lollo & Wilson, 1978).

Although an experiment of this type would be the best means of showing whether the duration effect is a result of the reduction in the apparent contrast of brief stimuli, the results of the experiments do provide some evidence that this is not the case. In each of Experiments 5, 7, 8 and 9, the shortest stimulus duration employed was 50 msec. This would not be expected to reduce the apparent contrast of a 4 c/deg grating with a critical duration of about 100 msec by more than half. For a grating of 0.44 contrast, this would produce an apparent contrast of approximately 0.22. Experiment 2 has shown that a decrease in the contrast of a 4 c/deg grating from 0.44 to 0.22 increases persistence duration by less than 10 msec. In comparison, decreasing the duration of the 4 c/deg presentation from 100 to 50 msec increases persistence duration by about 35 msec (see Figure 14). The effect on persistence duration of the reduction in the apparent contrast of briefly presented stimuli is consequently too small to account for the observed duration effect.

At low contrast levels a reduction in the duration of the presentation should have a greater effect on persistence than at high contrast levels. This is because small differences in contrast have a considerable effect on

persistence duration at low initial contrast levels (Experiment 2). The initial slope of the persistence x duration relationship should consequently be steeper for low than for high contrast levels. Although the slopes obtained in Experiment 8 were not as steep as would be expected, the lower contrast levels did produce steeper initial slopes than the higher contrast levels. It consequently appears that stimulus duration has an effect which is different from any effect it may have on persistence through the reduction in the apparent contrast of the stimulus presentation. It has been hypothesised that this duration effect is a result of the limited temporal resolution of the visual system at the peripheral level. A brief stimulus of any contrast should produce a neural response lasting for a specific time period which is relatively independent of both stimulus duration and intensity as long as its duration is shorter than the critical duration. Response persistence should consequently decrease linearly with increasing duration whether equal energy stimuli are employed or otherwise, contrary to Bowen et al. (1974).

The model presented in this thesis argues that persistence comprises components at both retinal and cortical levels. How these components combine to produce the overall percept of persistence is not clear. It is suggested that presentation of a stimulus may initiate a number of processes at the retinal ganglion cell level including a transient on-response and a more prolonged sustained response. Termination of the stimulus may be accompanied by an off-response which apparently does not affect the duration of the peripheral sustained response.

A cortical on-response which gives rise to the onset reaction time may be triggered by impulses from the peripheral transient cells. The pattern percept may follow once the longer cortical sustained response has been triggered. The cortical cells presumably continue to respond while they receive impulses from peripheral sustained mechanisms. The duration of the peripheral sustained response would thus determine that of the cortical response. In the absence of any further stimulation, cortical sustained cells may continue to respond for a period of time which is independent of the duration of the original stimulus. This additional activity would manifest itself as a second persistence component. Total persistence duration would then be a result of the total response time of cortical sustained neurones.

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APPENDIX A.

Raw data and summaries of the analyses of variance of the experiments.

Table A1. Individual persistence scores (msec) and summary of analysis of variance of Experiment 1.

		Low Contrast (0.07)					High Contrast (0.44)				
Spatial frequency (c/deg)		1	2	4	8	12	1	2	4	8	12
Subject No.	1	156	134	142	229	216	116	154	174	188	254
	2	358	179	214	355	412	196	188	182	289	309
	3	279	382	425	399	445	278	292	316	375	415
	4	116	101	186	186	*	114	106	106	115	188
	5	155	131	159	161	178	104	124	144	154	219
	6	157	152	221	216	278	85	79	122	249	335
	7	161	139	154	358	*	98	105	126	256	298
	8	121	119	135	136	141	82	75	112	86	196
	9	208	174	154	283	299	129	174	194	291	318
	10	581	516	456	681	727	314	446	282	436	498
	$\bar{X}$	229	203	224	301	337	152	174	175	244	299

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Contrast	54861.5	1	54861.5	6.61	0.03
Contrast x subjects	74693.7	9	8299.3		
Frequency	247869.9	4	61967.5	22.38	0.00
Frequency x subjects	99679.3	36	2768.9		
Contrast x frequency	9667.4	4	2416.9	2.09	0.10
Subjects	1200411.3	9	133379.0		
Error	41546.9	36	1222.0		

Table A2. Individual persistence scores (msec) and analysis of variance of the data of Experiment 2a.

		1 c/deg					4 c/deg				
Contrast level		0.03	0.11	0.22	0.33	0.44	0.03	0.11	0.22	0.33	0.44
Subject No.	1	267	191	188	193	223	295	250	170	183	180
	2	167	112	97	107	95	167	132	107	118	112
	3	143	137	127	122	125	195	147	152	127	170
	4	168	158	138	133	137	152	143	137	125	143
	5	145	140	140	135	142	174	128	173	148	132
	6	263	170	160	135	142	273	172	135	128	162
	7	258	247	173	157	165	190	230	178	178	205
	8	123	123	122	130	122	140	137	148	140	133
	9	252	240	270	163	148	278	255	215	215	188
	10	323	307	303	258	238	*	270	230	233	227
	$\bar{X}$	211	182	172	153	154	207	186	165	160	165

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Contrast	43070.8	4	10767.7	11.92	0.00
Contrast x subjects	32523.7	36	903.4		
Frequency	340.8	1	340.8	0.44	0.52
Frequency x subjects	6934.0	9	770.4		
Contrast x frequency	948.3	4	237.1	0.65	0.63
Subjects	204402.6	9	22711.4		
Error	13089.8	36	374.0		

Table A3. Individual persistence scores and summary of the analysis of variance of the data of Experiment 2b.

		4 c/deg					12 c/deg				
Contrast level		0.22	0.33	0.44	0.55	0.66	0.22	0.33	0.44	0.55	0.66
Subject No.	1	242	222	210	228	210	378	418	415	322	377
	2	120	115	108	107	103	453	404	381	298	180
	3	128	122	118	120	112	254	247	228	225	208
	4	115	115	122	105	108	*	308	297	213	213
	5	172	173	178	172	188	284	290	263	275	250
	6	118	122	105	112	103	185	182	180	175	180
	7	400	453	413	410	380	749	693	663	653	600
	8	117	130	123	120	112	*	182	208	209	183
	9	157	148	147	133	136	261	260	303	240	213
	10	240	203	178	188	205	297	320	320	340	277
	$\bar{X}$	181	180	170	170	166	336	330	326	295	268

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Contrast	24204.0	4	6051.0	8.56	0.00
Contrast x subjects	25444.8	36	706.8		
Frequency	474348.5	1	474348.5	46.27	0.00
Frequency x subjects	92262.2	9	10251.4		
Contrast x frequency	10864.4	4	2716.1	3.32	0.02
Subjects	1189552.9	9	132172.6		
Error	29437.2	36	817.7		

Table A4. Individual persistence scores (msec) and summary of the analysis of variance of the data of Experiment 3.

		0.44 Contrast				Matched apparent contrast			
Spatial frequency (c/deg)		2	4	8	16	2	4	8	16
Subject No.	1	167	148	180	272	178	157	172	273
	2	163	167	168	230	187	182	175	257
	3	177	175	185	233	207	198	213	232
	4	245	278	398	527	288	325	412	441
	5	335	353	407	496	305	353	455	646
	6	242	217	342	343	250	227	355	350
	7	120	95	138	183	122	113	128	210
	8	110	113	165	262	125	117	163	255
	$\bar{X}$	195	193	248	318	208	209	259	333

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Contrast	2983.9	1	2983.9	8.57	0.02
Contrast x subjects	2436.0	7	348.0		
Frequency	166490.3	3	55496.7	20.22	0.00
Frequency x subjects	57642.8	21	2744.9		
Contrast x frequency	47.9	3	16.0	0.02	0.99
Subjects	574340.6	7	82048.7		
Error	16155.7	21	769.3		

Table A5. Individual persistence scores (msec) and summary of the analysis of variance of the data of Experiment 4.

		Contrast level		
		1.0	0.8	0.6
Subject No.	1	318	323	316
	2	253	259	271
	3	123	126	124
	4	328	345	328
	5	185	159	204
	6	288	288	295
	7	279	273	258
	8	510	531	545
	$\bar{X}$	285	288	293

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Contrast	216.3	2	108.1	0.72	0.50
Subjects	299936.3	7	42848.0		
Contrast x subjects	2106.7	14	150.5		

Table A6 (i) Individual persistence scores (msec) for Experiment 5.

		1 c/deg						4 c/deg					
Stimulus duration (msec)		50	75	100	150	200	300	50	75	100	150	200	300
Subject No.	1	365	330	380	343	299	233	488	401	262	395	348	222
	2	122	100	83	88	83	62	117	132	120	120	112	95
	3	275	210	267	233	227	207	263	323	285	272	230	287
	4	188	170	188	172	182	187	250	208	225	218	208	155
	5	97	75	87	88	92	77	155	97	107	113	118	113
	6	125	142	120	130	152	113	122	138	162	142	143	162
	7	140	135	143	152	138	133	177	175	178	155	148	147
	8	213	170	142	132	175	170	163	193	190	212	193	222
	9	148	172	173	150	167	155	235	148	152	187	200	193
	10	243	203	210	260	177	160	348	272	227	233	237	203
	11	237	242	150	153	140	135	233	242	183	190	156	140
	12	213	230	210	248	163	172	305	237	227	245	233	228
	$\bar{X}$	197	182	179	179	166	150	238	214	193	207	194	181

		12 c/deg					
Stimulus duration (msec)		50	75	100	150	200	300
Subject No.	1	502	405	418	390	433	387
	2	152	160	140	137	125	127
	3	397	332	340	245	243	312
	4	338	378	318	263	263	188
	5	223	168	167	120	135	132
	6	188	157	157	182	140	133
	7	207	288	237	232	138	140
	8	387	277	312	272	267	270
	9	292	278	222	170	177	168
	10	378	368	330	277	228	210
	11	235	218	243	162	212	157
	12	335	348	258	293	232	218
	$\bar{X}$	303	281	262	229	216	204

Table A6 (ii). Summary of the analysis of variance of the data of Experiment 5.

ANALYSIS OF VARIANCE

Source of Variation	SS	df	MS	F	P
Frequency	196991.0	2	98495.5	56.64	0.00
Frequency x subjects	38256.2	22	1738.9		
Duration	104513.4	5	20902.7	17.08	0.00
Duration x subjects	67303.8	55	1223.7		
Frequency x duration	27043.0	10	2704.3	3.02	0.002
Subjects	1007335.9	11	91576.0		
Error	98636.4	110	896.7		

Table A7. Individual persistence scores (msec) and summary of the analysis of variance of the data of Experiment 6.

		Vertical				Oblique			
Spatial frequency (c/deg)		2	4	8	12	2	4	8	12
Subject No.	1	191	201	216	233	195	249	226	285
	2	194	225	286	358	244	283	310	336
	3	169	173	224	213	188	219	254	215
	4	273	286	424	470	270	319	516	428
	5	119	119	150	169	116	150	178	176
	6	90	124	156	151	109	126	149	148
	7	128	168	183	168	133	150	160	158
	8	173	188	233	265	163	193	266	266
	$\bar{X}$	167	185	234	253	177	211	257	251

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Orientation	3299.1	1	3299.1	8.54	0.02
Orientation x subjects	2704.5	7	386.4		
Frequency	71008.8	3	23669.6	12.64	0.00
Frequency x subjects	39317.1	21	1872.2		
Orientation x frequency	1960.8	3	653.6	1.80	0.18
Subjects	355089.3	7	50727.0		
Error	7627.8	21	363.2		

Table A8. Individual persistence scores (msec) and summary of the analysis of variance of the data of Experiment 7.

	Vertical						Oblique					
Stimulus duration (msec)	50	75	100	150	200	300	50	75	100	150	200	300
Subject No. 1	236	249	210	185	204	186	288	256	243	234	233	201
2	246	234	221	201	189	175	241	263	221	201	201	181
3	145	156	153	170	136	150	165	173	160	168	131	158
4	179	170	159	143	133	169	178	193	169	161	156	160
5	209	228	190	193	193	171	211	216	200	208	211	200
6	165	141	143	126	119	126	171	144	148	146	154	143
7	206	206	150	154	131	120	223	216	181	185	183	166
8	338	308	269	231	215	206	335	326	274	246	261	239
$\bar{X}$	215	211	187	175	165	163	226	223	199	194	191	181

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Orientation	3299.1	1	3299.1	8.54	0.02
Orientation x subjects	2704.5	7	386.4		
Frequency	71008.8	3	23669.6	12.64	0.00
Frequency x subjects	39317.1	21	1872.2		
Orientation x frequency	1960.8	3	653.6	1.80	0.18
Subjects	355089.3	7	50727.0		
Error	7627.8	21	363.2		

Table A9 (i). Individual persistence scores (msec) for Experiment 8.

High Contrast

Stimulus duration (msec)		Vertical						Oblique					
		50	75	100	150	200	300	50	75	100	150	200	300
Subject No.	1	108	110	125	85	79	64	115	92	93	85	90	69
	2	144	129	131	135	143	148	145	145	154	140	129	156
	3	329	256	244	228	235	209	393	290	270	264	260	218
	4	231	259	194	236	195	205	239	249	226	270	233	230
	5	114	84	56	36	41	30	123	60	86	49	48	38
	6	220	216	215	194	193	189	224	216	213	189	191	190
	7	231	223	239	208	216	196	251	235	280	276	231	234
	8	113	120	101	70	68	54	106	126	111	79	74	64
–	$\bar{x}$	**186**	**175**	**163**	**149**	**146**	**137**	**200**	**177**	**179**	**169**	**157**	**150**

Low contrast

Stimulus duration (msec)		Vertical						Oblique					
		50	75	100	150	200	300	50	75	100	150	200	300
Subject No.	1	125	121	111	100	80	73	123	125	125	89	74	54
	2	175	158	151	156	178	160	181	168	158	155	158	148
	3	360	289	303	284	241	188	413	325	306	269	220	216
	4	258	254	223	236	218	211	265	309	258	249	245	255
	5	126	91	65	50	69	53	146	90	101	70	53	50
	6	233	235	248	203	205	186	266	234	238	221	206	181
	7	353	376	339	353	318	241	346	385	360	319	320	248
	8	118	116	113	74	66	54	116	118	118	76	79	59
	$\bar{x}$	**219**	**205**	**194**	**182**	**172**	**146**	**232**	**219**	**208**	**181**	**169**	**151**

Table A9 (ii). Summary of the overall analysis of variance and of the analysis of variance of the high contrast data of Experiment 8.

ANALYSIS OF VARIANCE
(square root transform)

Source of variation	SS	df	MS	F	P
Contrast	33.98	1	33.98	7.92	0.03
Contrast x subjects	30.02	7	4.29		
Orientation	5.79	1	5.79	8.05	0.03
Orientation x subjects	5.03	7	0.72		
Duration	139.50	5	27.90	13.49	0.00
Duration x subjects	72.41	35	2.07		
Contrast x orientation	0.50	1	0.50	1.71	0.23
Contrast x orientation x subjects	2.04	7	0.29		
Contrast x duration	4.81	5	0.96	3.42	0.01
Contrast x duration x subjects	9.86	35	0.28		
Orientation x duration	1.01	5	0.20	0.86	0.52
Orientation x duration x subjects	8.19	35	0.23		
Contrast x orientation x duration	1.88	5	0.38	2.21	0.08
Subjects	1922.58	7	274.65		
Error	5.96	35	0.17		

ANALYSIS OF VARIANCE (High contrast data)
(square root transform)

Source of variation	SS	df	MS	F	P
Orientation	4.84	1	4.84	8.16	0.02
Orientation x subjects	4.15	7	0.59		
Duration	48.47	5	9.69	7.59	0.00
Duration x subjects	44.72	35	1.28		
Orientation x duration	1.41	5	0.28	1.44	0.23
Subjects	874.04	7	124.86		
Error	6.86	35	0.20		

Table A9 (iii). Summaries of the analyses of variance of the low contrast, vertical and oblique data of Experiment 8.

ANALYSIS OF VARIANCE (Low contrast data)

(Square root transform)

Source of variation	SS	df	MS	F	P
Orientation	1.44	1	1.44	3.46	0.11
Orientation x subjects	2.92	7	0.42		
Duration	95.84	5	19.17	17.87	0.00
Duration x subjects	37.55	35	1.07		
Orientation x duration	1.48	5	0.30	1.42	0.24
Subjects	1078.57	7	154.08		
Error	7.30	35	0.21		

ANALYSIS OF VARIANCE (Vertical data)

(Square root transform)

Source of variation	SS	df	MS	F	P
Contrast	21.36	1	21.36	6.85	0.03
Contrast x subjects	21.84	7	3.12		
Duration	67.03	5	13.41	11.88	0.00
Duration x subjects	39.51	35	1.13		
Contrast x duration	1.25	5	0.25	1.19	0.33
Subjects	913.67	7	130.52		
Error	7.32	35	0.21		

ANALYSIS OF VARIANCE (Oblique data)

(Square root transform)

Source of variation	SS	df	MS	F	P
Contrast	13.12	1	13.12	8.98	0.02
Contrast x subjects	10.23	7	1.46		
Duration	73.48	5	14.70	12.52	0.00
Duration x subjects	41.10	35	1.17		
Contrast x duration	5.44	5	1.09	4.48	0.00
Subjects	1013.94	7	144.85		
Error	8.50	35	0.24		

Table A10. Individual persistence scores (msec) and summary of the analysis of variance of the data of Experiment 9.

		Sine-wave						Square-wave					
Stimulus duration (msec)		50	75	100	150	200	300	50	75	100	150	200	300
Subject No.	1	290	254	241	211	190	199	293	241	231	211	221	204
	2	263	213	215	171	198	200	246	193	204	201	186	213
	3	245	254	220	211	191	219	250	231	195	206	200	174
	4	231	221	234	228	220	191	219	221	250	235	224	196
	5	229	203	188	160	171	160	229	201	186	161	174	173
	6	258	238	215	218	211	195	265	239	239	221	210	204
	7	188	141	146	128	124	123	219	139	128	131	141	129
	8	425	356	369	343	324	285	398	350	339	330	290	294
	$\bar{X}$	266	235	228	209	204	196	265	227	221	212	206	198

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Luminance profile	50.32	1	50.32	0.20	0.67
Luminance profile x subjects	1766.04	7	252.29		
Duration	48183.48	5	9636.70	22.08	0.00
Duration x subjects	15272.29	35	436.35		
Luminance profile x duration	488.61	5	97.72	0.84	0.53
Subjects	263713.54	7	37673.36		
Error	4053.66	35	115.82		

Table A11 (i) Individual contrast thresholds for Experiment 10.

Vertical

Subject No.	Stimulus duration (msec) 20	40	60	80	100	150	200	300	500	1000
1	1.53	1.31	1.17	1.11	1.03	0.97	0.91	0.92	0.81	0.85
2	1.75	1.55	1.36	1.31	1.28	1.24	1.22	1.21	1.12	1.07
3	1.72	1.46	1.32	1.29	1.15	1.08	1.03	0.95	0.96	0.92
4	1.26	1.03	0.85	0.79	0.73	0.69	0.65	0.58	0.54	0.53
5	1.24	1.13	1.02	0.97	0.83	0.68	0.73	0.59	0.55	0.47
6	1.48	1.31	1.31	1.21	1.21	1.07	1.13	0.91	0.93	0.93
7	1.60	1.33	1.20	1.11	1.05	0.98	0.94	0.88	0.87	0.93
8	1.67	1.53	1.34	1.29	1.19	1.09	1.12	1.07	0.95	0.93

Oblique

Subject No.	Stimulus duration (msec) 20	40	60	80	100	150	200	300	500	1000
1	1.67	1.42	1.31	1.21	1.14	1.09	1.05	1.00	0.98	0.96
2	1.72	1.44	1.32	1.26	1.22	1.13	1.09	1.13	1.03	1.06
3	1.77	1.63	1.43	1.39	1.28	1.08	1.03	1.05	0.94	0.94
4	1.33	1.07	0.94	0.83	0.80	0.74	0.65	0.63	0.61	0.57
5	1.31	1.19	1.06	0.97	0.85	0.75	0.70	0.70	0.65	0.55
6	1.46	1.36	1.28	1.19	1.29	1.07	1.03	1.03	0.98	0.93
7	1.64	1.42	1.20	1.20	1.06	1.13	0.96	0.98	0.92	0.99
8	1.73	1.53	1.42	1.16	1.12	1.14	1.03	1.12	1.07	1.00

(ii). Critical durations and slopes of the log intensity x log duration relationships, for individual subjects.

Subject No.	Critical duration		Slopes: Primary		Slopes: Secondary	
	Vertical	Oblique	Vertical	Oblique	Vertical	Oblique
1	106	106	-0.78	-0.79	-0.19	-0.18
2	72	76	-0.79	-0.77	-0.23	-0.22
3	126	186	-0.78	-0.79	-0.22	-0.18
4	74	86	-0.85	-0.85	-0.27	-0.25
5	146	143	-0.79	-0.79	-0.29	-0.22
6	245	158	-0.41	-0.43	-0.22	-0.16
7	105	101	-0.85	-0.83	-0.13	-0.13
8	120	133	-0.69	-0.73	-0.25	-0.12
$\bar{x}$	124	124	-0.74	-0.75	-0.23	-0.18

Table A12. Individual persistence scores (msec) for the adaptation experiments

(i) Experiment 11.

(ii) Experiment 12.

(i)

Subject No.	Adaptation Stimulus: Blank field	Stationary grating	Counterphase flickering grating
1	259	176	186
2	249	216	206
3	318	247	234
4	169	132	137
5	179	169	137
6	127	109	123
$\bar{x}$	200	175	171

(ii)

Subject No.	Adaptation Stimulus: Blank field	Flickering field
1	125	140
2	125	134
3	133	136
4	165	153
5	128	142
6	92	103
7	118	127
8	158	133
9	68	102
10	159	164
11	184	188
12	138	171
13	225	210
14	194	200
$\bar{x}$	145	150

Table A13. Individual blank field detection thresholds (msec) and summary of the analysis of variance of the data of Experiment 13.

		1 c/deg				4 c/deg				8 c/deg			
Stimulus duration (msec)		50	100	200	400	50	100	200	400	50	100	200	400
Subject No.	1	64	60	40	60	26	25	27	26	50	40	40	120
	2	58	18	27	43	88	64	55	67	108	113	112	132
	3	66	70	45	35	35	33	30	43	100	92	113	120
	4	85	80	80	78	73	45	60	73	165	160	150	140
	5	25	18	25	25	20	23	20	18	65	60	60	55
	6	5	25	23	26	8	13	20	16	25	43	50	44
	7	40	20	26	24	20	20	17	43	67	50	50	44
	8	80	60	30	28	60	40	33	26	100	100	100	95
	$\bar{X}$	53	44	37	40	41	33	33	39	85	82	84	84

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Frequency	46712.25	2	23356.13	23.43	0.00
Frequency x subjects	13954.75	14	996.77		
Duration	1082.61	3	360.87	1.61	0.22
Duration x subjects	4965.47	21	223.59		
Frequency x duration	1130.92	6	188.49	1.23	.31
Subjects	50752.41	7	7250.34		
Error	6452.75	42	153.64		

Table A14. Individual blank field detection thresholds (msec) and summary of the analysis of variance of the data of Experiment 14.

		1 c/deg				4 c/deg				8 c/deg			
Stimulus duration (msec)		50	100	200	400	50	100	200	400	50	100	200	400
Subject No.	1	10	18	40	55	13	14	13	20	5	30	15	28
	2	16	40	30	48	5	15	23	20	10	20	33	43
	3	10	13	20	18	5	10	25	24	25	15	27	87
	4	70	93	90	120	50	57	43	80	90	140	225	145
	5	5	8	10	15	8	8	25	13	18	38	28	33
	6	33	17	107	270	60	47	60	100	120	60	130	133
	7	13	20	16	14	8	30	18	15	20	50	70	40
	8	14	17	20	50	18	30	24	26	67	80	110	132
	$\bar{X}$	21	28	42	74	21	26	29	37	44	54	80	80

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Frequency	21606.02	2	10803.01	7.53	0.006
Frequency x subjects	20076.81	14	1434.06		
Duration	17091.04	3	5697.01	5.75	0.005
Duration x subjects	20801.46	21	990.55		
Frequency x duration	4900.90	6	816.82	1.32	0.272
Subjects	96747.13	7	13821.02		
Error	26077.60	42	620.90		

Table A15 Individual blank field detection thresholds (msec) and summary of the analysis of variance of the data of Experiment 15.

		1 c/deg				4 c/deg				8 c/deg			
Stimulus duration (msec)		50	100	200	400	50	100	200	400	50	100	200	400
Subject No.	1	50	45	50	25	15	15	20	18	70	60	45	50
	2	110	85	87	72	78	53	80	84	152	80	140	60
	3	30	43	58	20	35	18	35	35	66	47	20	30
	4	25	8	17	17	7	9	7	20	30	40	40	43
	5	133	107	95	105	160	145	140	115	260	370	268	220
	6	40	47	60	93	75	40	72	60	135	110	120	110
	7	30	25	40	55	60	60	55	54	115	120	70	105
	8	110	35	38	16	127	80	40	67	105	107	80	53
	$\bar{X}$	66	49	56	50	70	53	56	57	117	117	98	84

ANALYSIS OF VARIANCE (Log transform)

Source of variation	SS	df	MS	F	P
Frequency	8.341	2	4.171	10.72	0.002
Frequency x subjects	5.448	14	0.389		
Duration	0.792	3	0.264	1.91	0.159
Duration x subjects	2.905	21	0.138		
Frequency x duration	0.888	6	0.148	1.41	0.233
Subjects	38.426	7	5.489		
Error	4.406	42	0.105		

Table A16. Individual blank field detection thresholds (msec) and summary of the analysis of variance of the data of Experiment 16.

		1 c/deg				4 c/deg				8 c/deg			
Stimulus duration (msec)		50	100	200	400	50	100	200	400	50	100	200	400
Subject No.	1	130	190	115	130	350	160	75	70	500	250	400	200
	2	48	30	15	15	35	40	15	16	120	77	40	25
	3	40	64	38	23	8	20	15	10	90	35	55	40
	4	20	38	18	30	13	8	15	18	50	55	60	45
	5	25	33	15	16	7	10	23	20	40	85	125	100
	6	160	90	110	112	100	60	50	28	160	120	140	115
	7	70	55	25	25	60	45	35	27	180	115	90	65
	8	20	23	26	20	73	40	20	17	40	120	50	80
	$\bar{X}$	64	45	45	46	81	48	31	26	148	107	120	84

ANALYSIS OF VARIANCE (Log transform)

Source of variation	SS	df	MS	F	P
Frequency	20.947	2	10.474	28.61	0.000
Frequency x subjects	5.125	14	0.366		
Duration	3.045	3	1.015	4.18	0.018
Duration x subjects	5.094	21	0.243		
Frequency x duration	0.460	6	0.077	0.50	0.801
Subjects	40.368	7	5.767		
Error	6.381	42	0.152		

Table A17. Individual offset-onset reaction time differences (msec) and summary of the analysis of variance of this difference (Expt. 17).

2 c/deg

Subject No.	Stimulus duration (msec) 40	60	80	100	150	200	300
1	142	138	108	122	88	132	97
2	141	153	157	108	96	142	82
3	175	139	154	108	178	155	158
4	130	174	134	113	143	117	107
5	171	124	108	150	63	67	47
6	164	157	135	93	84	108	103
7	203	169	140	125	72	123	46
8	140	135	91	61	74	95	83
$\bar{X}$	158	149	128	110	100	117	90

8 c/deg

Subject No.	Stimulus duration (msec) 40	60	80	100	150	200	300	500
1	142	145	142	120	92	88	77	52
2	172	155	138	112	72	113	122	106
3	175	173	169	176	179	166	213	222
4	158	147	167	119	159	108	84	74
5	126	128	124	116	118	51	91	86
6	130	149	152	122	127	135	82	66
7	209	150	129	104	147	130	24	90
8	163	106	108	88	70	51	44	111
$\bar{X}$	159	144	141	120	121	105	92	101

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Frequency	493.08	1	493.08	1.42	0.27
Frequency x subjects	2429.99	7	347.00		
Duration	53416.46	6	8902.74	9.95	0.00
Duration x subjects	37562.54	42	894.35		
Frequency x duration	2936.36	6	489.39	1.15	0.35
Subjects	43750.78	7	6250.11		
Error	17938.07	42	427.10		

Table A18. Individual onset and offset reaction times (msec) from Experiment 18 and summaries of analyses of variance of onset and offset reaction time, and of offset-onset reaction time difference.

		Onset reaction time					Offset reaction time				
Spatial frequency (c/deg)		2	4	6	8	12	2	4	6	8	12
Subject No.	1	288	309	309	319	400	355	326	336	393	342
	2	423	414	438	443	444	378	400	401	435	409
	3	308	300	324	339	350	406	384	393	403	423
	4	308	335	339	334	346	352	355	379	385	384
	5	270	279	284	287	290	397	396	401	408	404
	6	302	311	316	322	341	303	334	343	357	325
	$\bar{X}$	317	325	335	341	362	365	366	376	397	381

ANALYSES OF VARIANCE

1) Onset reaction time

Source of variation	SS	df	MS	F	P
Frequency	7190.87	4	1797.72	7.62	0.00
Subjects	63957.47	5	12791.49		
Error	75869.87	20	236.08		

2) Offset reaction time

Source of variation	SS	df	MS	F	P
Frequency	4065.87	4	1016.47	5.11	0.005
Subjects	23475.50	5	4695.10		
Error	3975.33	20	198.77		

3) Offset-onset reaction time difference

Source of variation	SS	df	MS	F	P
Frequency	4550.33	4	1137.58	2.12	0.12
Subjects	65830.97	5	13166.19		
Error	10714.87	20	2796.42		

Table A19. Onset and offset reaction times (msec) for Experiment 19 and summary of the analysis of variance of the individual offset-onset reaction time differences.

		Onset reaction time				Offset reaction time			
Spatial frequency (c/deg)		1	2	4	8	1	2	4	8
Subject No.	1	241	244	246	263	333	322	337	348
	2	380	378	350	353	566	618	727	638
	3	271	279	268	290	518	536	635	618
	4	303	270	280	290	478	476	428	495
	5	278	294	303	340	487	524	518	509
	6	304	291	308	269	380	395	419	455
	7	253	262	273	278	338	361	332	359
	8	332	316	331	331	700	566	563	620
	$\bar{X}$	295	292	295	302	475	475	495	505

ANALYSIS OF VARIANCE

Source of variation	SS	df	MS	F	P
Frequency	3532.84	3	1177.61	0.49	0.69
Subjects	227253.47	7	32464.78		
Error	49740.91	21	9049.27		

APPENDIX B.

Published papers.

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The effect of spatial frequency and contrast on visual persistence

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Abstract. The visual persistence of sinusoidal gratings of varying spatial frequency and contrast was measured. It was found that the persistence of low-contrast gratings was longer than that of high-contrast stimuli for all spatial frequencies investigated. At higher contrast levels of 1 and 4 cycles deg^{-1} gratings, a tendency for persistence to be independent of contrast was observed. For 12 cycles deg^{-1} gratings, however, persistence continued to decrease with increasing contrast. These results are compared with recently published data on other temporal responses, and are discussed in terms of the different properties of sustained and transient channels.

1 Introduction

It has been shown that a trace of a briefly presented stimulus persists in the visual system for some time after the offset of the stimulus (e.g. Haber and Standing 1970). This trace, which decays rapidly with time, has been viewed as a temporary memory store in which information is retained prior to coding (e.g. Sperling 1960). The names 'visual information store' (VIS), and 'iconic memory' or 'icon' reflect this idea. The effect has also been thought to be due to the continuation of neural activity associated with stimulus processing beyond the offset of the stimulus (Di Lollo 1977). Hence, the phenomenon is also known as 'visual persistence' (Ganz 1975). Because neural activity lasts for a particular length of time, the neurons responding to a stimulus may remain active for some time after stimulus offset, causing a neural representation of the stimulus to persist. This may be especially true for stimuli of relatively short duration (Di Lollo 1977; Haber and Standing 1970). Evidence that persistence has a neurological basis has been obtained from studies implicating the involvement of cortical orientation-specific neurons in this (Meyer et al 1975; Meyer 1977). Under some circumstances, however, persistence may also be a retinal phenomenon (Sakitt 1975).

The duration of the persistence of gratings has been found to depend upon the spatial frequency of the stimuli. Meyer and Maguire (1977) have shown that the persistence of 50 ms duration, high-contrast square-wave gratings increased monotonically with spatial frequency. Recently, spatial frequency has also been shown to influence other temporal factors, such as critical duration and the summation function, which appear to be related to persistence (Ganz 1975). For stimulus presentations shorter than a specific critical duration the threshold intensity of a stimulus is reciprocally related to its duration (Bloch's Law). It has recently been shown that the length of this critical duration is dependent upon the nature of the stimulus, being longer for stimuli of higher spatial frequency than it is for lower-spatial-frequency stimuli (Breitmeyer and Ganz 1977; Legge 1978). The shape of the interaction between two briefly presented stimuli (the summation function) has also been shown to depend upon the spatial frequency of the stimuli (Watson and Nachmias 1977). At low frequencies, the period of temporal summation is brief, and is followed by a pronounced inhibitory phase. At higher frequencies, the time over which summation occurs is longer, and the inhibitory phase is reduced, or is absent altogether.

Recently attempts have been made to relate these temporal factors to two distinct classes of cells which differ in their temporal properties and in the spatial frequencies to which they are maximally responsive. Legge (1978) has recently reviewed the psychophysical evidence for the existence of these 'sustained' and 'transient' channels. Transient channels are characterised by transient responses to the onset and offset of a stimulus (Tolhurst 1975b). They are highly responsive to movement or flicker (Kulikowski and Tolhurst 1973), and predominate at low spatial frequencies (Tolhurst 1975a, 1975b). Sustained channels are characterised by a sustained response to a stimulus, predominate at high spatial frequencies, and respond more specifically to pattern than to movement (Kulikowski and Tolhurst 1973; Tolhurst 1975a, 1975b). Sustained channels also appear to have longer response latencies than transient channels (Breitmeyer 1975b; Lupp et al 1976; Vassilev and Mitov 1976). This difference between sustained and transient channels has been thought to be the mechanism underlying the spatial-frequency-dependent variation in the temporal properties discussed above (Breitmeyer and Ganz 1977; Meyer and Maguire 1977; Watson and Nachmias 1977). Low-spatial-frequency stimuli predominantly stimulate transient channels. These appear to respond more quickly than sustained channels, which are activated by higher spatial frequencies.

Meyer et al (1975) and Meyer (1977) using adaptation procedures have demonstrated that cortical elements may be involved in persistence. They hypothesised that adaptation to a grating of a specific orientation would result in a decrease in the persistence of a test grating of the same orientation owing to the reduced apparent contrast of this grating (Blakemore et al 1973). A decrease in the persistence of square-wave gratings was subsequently observed after adaptation to gratings of the same orientation. This reduction in persistence was not obtained when adaptation and test gratings differed by 90°. Although these experiments have shown that adaptation results in reduced persistence they did not provide any direct evidence that the contrast of the stimulus has any effect on persistence. It is possible that contrast has no effect, and that the adaptation results obtained by Meyer et al (1975) and Meyer (1977) occur as a result of a mechanism other than the reduction in apparent contrast.

The following experiments were accordingly performed to test the hypothesis that low-contrast gratings have shorter persistence than higher-contrast stimuli, and to investigate further the relationship between persistence and spatial frequency. The higher harmonics contained in the high-contrast square-wave gratings used by Meyer and Maguire (1977) may have influenced persistence. Since the simplest stimuli analysed by the visual system appear to be sinusoidal gratings (Campbell and Robson 1968), this waveform was used in the present experiments unless otherwise indicated. The contrast range of the sinusoidal stimuli was kept relatively low, to prevent distortion of the waveform. It was hypothesised that an increase in persistence with spatial frequency similar to that obtained by Meyer and Maguire (1977) would occur with sinusoidal stimuli of relatively low contrast.

2 Method, experiments 1, 2a, and 2b

2.1 *Apparatus*

Stimuli were presented by means of a Scientific Prototype three-channel tachistoscope. The stimuli were photographic reproductions of oscilloscope-generated sinusoidal gratings. The contrast of all gratings was estimated from a plot of Michelson contrast (obtained by measuring the maximum and minimum luminances of projected photographic negatives of gratings) against the output level of the oscilloscope (in volts). The space-average luminance of all gratings and of the blank with which they alternated was kept constant at 9 cd m^{-2}.

2.2 *Subjects*
These were volunteers predominantly recruited from undergraduate psychology classes and were unfamiliar with the hypotheses. All had normal or corrected-to-normal vision.

2.3 *Procedure*
Persistence was measured by a method similar to that of Meyer et al (1975). The stimulus presentation was viewed binocularly. Each grating stimulus was presented for 50 ms, and was alternated with a variable blank interstimulus interval (ISI) for ten cycles. The duration of the ISI was altered in 10 ms steps, except at very long ISIs (350 ms or more) when 20 ms steps were employed. Subjects were requested to report whether a distinct blank interval appeared between each grating cycle of the presentation. They were asked to report detection of the blank only if the grating appeared to fade completely between each cycle. A random staircase method was employed to obtain each subject's threshold for detection of the blank interval, the ISI being increased or decreased according to the subject's response on the previous trial. After each threshold reversal the ISI was either increased or decreased by 10 ms according to a previously randomised sequence. The initial ISI duration for each block of trials was chosen so that it was either considerably above or considerably below each subject's approximate detection threshold as determined during practice. Each block of trials consisted of six threshold reversals. The mean of these six threshold reversals for each stimulus was taken to be its persistence measurement. Data for each subject were obtained in a single experimental session which comprised an initial block of practice trials followed by the experimental trials.

3 Experiment 1
This experiment was designed to extend the results of Meyer and Maguire (1977) but with sinusoidal gratings and two levels of contrast. Repeated measures were taken over both factors. The spatial frequencies of the stimuli were 1, 2, 4, 8, and 12 cycles deg^{-1} and the Michelson contrast levels were 0·44 and 0·07. A circular field, subtending 5 deg of visual angle was used. Ten subjects participated and the order of presentation of the stimuli was counterbalanced according to a 10 x 10 Latin square.

3.1 *Results*
Mean persistence is shown in figure 1 as a function of spatial frequency at both contrast levels. Persistence increased linearly with spatial frequency at both contrast levels. A considerable difference between the overall means of the high- and low-contrast data was obtained, the persistence of the low-contrast stimuli being longer than that of the high-contrast stimuli. The analysis of variance showed that this difference between the contrast levels was significant ($F_{1,9} = 6{\cdot}3$; $p < 0{\cdot}05$). There was no significant interaction between contrast and spatial frequency ($F_{4,34} = 1{\cdot}7$; $p > 0{\cdot}05$) but the main effect of spatial frequency was highly significant ($F_{4,36} = 21{\cdot}3$; $p < 0{\cdot}001$). Comparisons between the means with the use of Duncan's new multiple range test indicated that at both contrast levels the 12 and 8 cycles deg^{-1} gratings produced significantly longer persistence ($p < 0{\cdot}01$) than the 1, 2, and 4 cycles deg^{-1} gratings, which did not differ significantly from each other. In addition the persistence of the 12 cycles deg^{-1} grating was significantly longer ($p < 0{\cdot}01$) than that of the 8 cycles deg^{-1} stimulus at the high contrast level. The difference between the overall means of the two contrast levels was 45 ms, and regression coefficients for the low- and high-contrast data were 11·9 and 13·2 respectively.

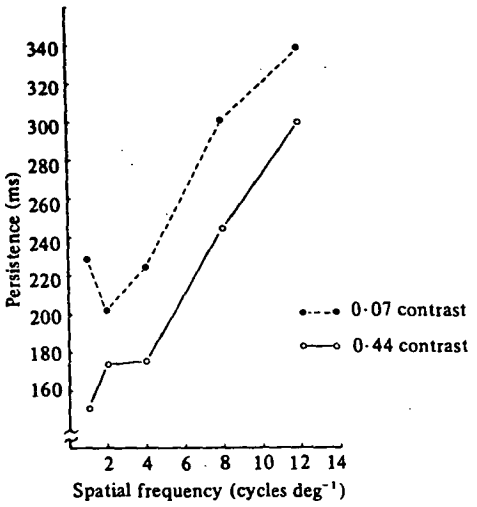

Figure 1. Mean persistence of two contrast levels of a sinusoidal grating as a function of the spatial frequency of the grating.

3.2 *Discussion*

The results of this experiment are in agreement with the findings of Meyer and Maguire (1977) that persistence increases with spatial frequency. A substantial increase in persistence with increasing spatial frequency was obtained for both low-contrast (0·07) and high-contrast (0·44) sinusoidal gratings. There was, however, some difference between the two experiments in mean persistence at each spatial frequency. Mean persistence increased from approximately 300 ms at 0·9 cycle deg^{-1} to 500 ms at 15 cycles deg^{-1} in the Meyer and Maguire (1977) experiment, while for the high-contrast condition in the current experiment it increased from 150 to 300 ms over a similar range of spatial frequencies (1–12 cycles deg^{-1}). This difference may be due to the differences between the luminance profiles employed in the two experiments although other factors such as field size or individual differences could be important. Individual subjects varied from each other by as much as 200–300 ms in judgements of ISI duration at each spatial frequency in the present experiment. This apparently occurred as a result of differing criteria employed by different subjects.

The finding that the persistence of low-contrast gratings was longer rather than shorter than that of high-contrast stimuli was contrary to the hypothesis. In order to obtain further information to provide a possible explanation for this effect, the relationship between contrast and persistence was investigated by examining the effect of a range of contrasts upon persistence. This was done in experiment 2.

4 Experiment 2

This comprised two similar experiments, in both of which five contrast levels were used at each of two spatial frequencies. In experiment 2a the contrast levels were 0·03, 0·11, 0·22, 0·33, and 0·44 at 1 and 4 cycles deg^{-1}. A 5 deg diameter field size was used. In experiment 2b, with spatial frequencies of 4 and 12 cycles deg^{-1}, contrast varied in steps of 0·11 units from 0·22 to 0·66. These higher contrast levels were necessary in this experiment since the alternating 12 cycles deg^{-1} grating was not readily visible to many subjects at contrasts lower than 0·22. The field size was 2 deg. Ten subjects participated in each experiment.

4.1 *Results*

The mean persistences for both experiments are shown in figures 2a and 2b as a function of contrast. The data for each spatial frequency are plotted separately. In general, a tendency for persistence to decrease with increasing contrast was observed for all spatial frequencies, although at lower spatial frequencies (1 and 4 cycles deg^{-1}) there was little effect of contrast upon persistence at levels above 0·22.

The analysis of variance of the data from experiment 2a gave a significant contrast effect ($F_{4,36} = 11{\cdot}9$; $p < 0{\cdot}001$). Neither the spatial-frequency main effect ($F_{1,36} = 0{\cdot}44$; $p > 0{\cdot}05$) nor the spatial-frequency x contrast interaction ($F_{4,36} = 0{\cdot}65$; $p > 0{\cdot}05$) was significant. The Duncan test revealed that the persistence of the 0·03 contrast grating was significantly longer ($p < 0{\cdot}01$) than that of all the other contrast levels at both 1 and 4 cycles deg^{-1}. The 0·11 contrast was also significantly more persistent ($p < 0{\cdot}01$) than the 0·33 and 0·44 contrast levels at 1 cycle deg^{-1}, and than the 0·33 contrast at 4 cycles deg^{-1}. There was no significant difference between the persistence of the 0·22, 0·33, and 0·44 contrast levels. Thus the effect of contrast upon persistence was most pronounced at low contrast levels.

The analysis of variance of the data from experiment 2b gave significant spatial-frequency ($F_{1,36} = 46{\cdot}3$; $p < 0{\cdot}001$) and contrast ($F_{4,36} = 8{\cdot}6$; $p < 0{\cdot}001$) effects. A significant spatial-frequency x contrast interaction was also obtained ($F_{4,36} = 3{\cdot}3$; $p < 0{\cdot}05$). The Duncan test revealed no significant differences in persistence between any of the contrast levels of the 4 cycles deg^{-1} grating. At 12 cycles deg^{-1}, the 0·66 contrast level produced significantly less persistence ($p < 0{\cdot}01$) than the 0·44, 0·33, and 0·22 contrast levels, which did not differ significantly from each other. The persistence of the 0·55 contrast level was, however, significantly shorter ($p < 0{\cdot}01$) than that of the 0·22 contrast level.

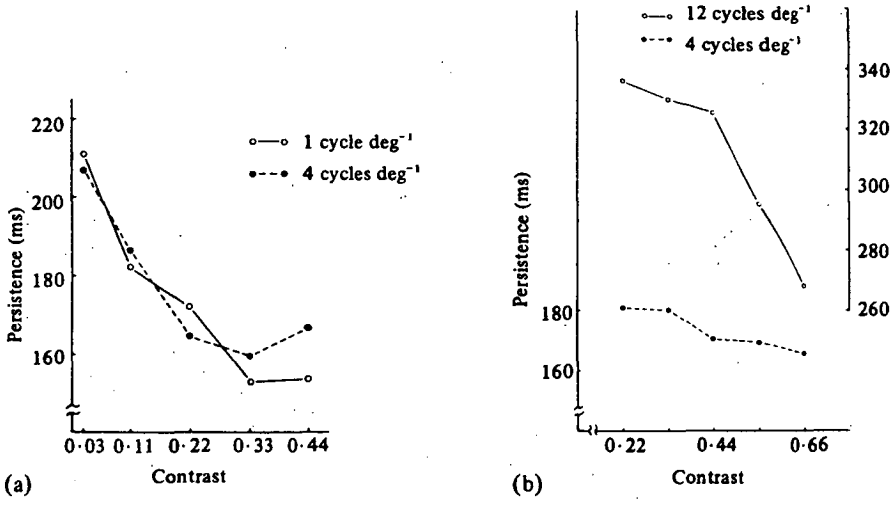

Figure 2. Mean persistence as a function of grating contrast: (a) 1 and 4 cycles deg^{-1} gratings; (b) 4 and 12 cycles deg^{-1} gratings.

4.2 *Discussion*

The results of these experiments indicate that persistence is elevated at low contrasts for each of the spatial frequencies investigated. At low spatial frequencies (1 and 4 cycles deg^{-1}) persistence appeared to be elevated only at low contrasts, becoming independent of changes in contrast at contrasts above 0·22. No effect of contrast on persistence was obtained for the higher-contrast 4 cycles deg^{-1} gratings employed in experiment 2b. The decline in the persistence of low-frequency sinusoidal gratings with increasing contrast thus appears to asymptote as contrast increases.

Although the persistence of the 12 cycles deg^{-1} stimuli also declined with increasing contrast, no tendency to asymptote was observed, persistence continuing to decrease as contrast increased. However, the highest contrast (0·66) employed in this experiment may not have been great enough for the graph to asymptote as a function of contrast. The effect of contrast on the persistence of the 12 cycles deg^{-1} grating at medium contrasts was small and nonsignificant. This nonsignificant effect may have been an artifact due to the difficulty some subjects experienced in perceiving the grating at low contrasts.

The continued decline in the persistence of the 12 cycles deg^{-1} grating at contrasts which had no further effect on that of 4 cycles deg^{-1} stimuli may partly result from a reduction in the apparent contrast of the 12 cycles deg^{-1} stimulus observed under the conditions of the experiment. It is possible that the apparent contrast of even the highest-contrast 12 cycles deg^{-1} grating may have been low enough during alternation to be similar to that of the low-contrast 1 and 4 cycles deg^{-1} stimuli. The relative contributions of sustained and transient mechanisms to persistence may also account for the difference in the shapes of the contrast x persistence relationship between spatial frequencies (see general discussion).

5 Experiment 3

The present results indicate that reducing the contrast of a stimulus is likely to increase persistence rather than to decrease it. Thus, it may be necessary to postulate that a mechanism other than contrast reduction is responsible for the adaptation results of Meyer et al (1975). The experimental conditions used by Meyer et al (1975) were, however, somewhat different from those employed in experiments 1 and 2 of this paper. They used high-contrast (0·97) square-wave gratings, whereas low- to medium-contrast sinusoidal gratings were employed in the present experiments. In addition, they used a 3 deg by 5·5 deg field size, luminance during testing was 1·42 foot lamberts (4·9 cd m^{-2}), and the spatial frequency of their test stimulus was 6·5 cycles deg^{-1}. These differences between the two groups of experiments may enable their explanation to be valid under their experimental conditions. It is, for example, possible that contrast has a nonmonotonic effect on persistence. In this case, decreased persistence would be expected to result from contrast reduction at the high-contrast levels employed by Meyer et al (1975).

This experiment was therefore carried out under experimental conditions as similar as possible to those used by Meyer et al (1975). The stimulus was a 6·5 cycles deg^{-1} square-wave grating with a contrast as close to 1·0 as could be obtained. The two lower contrast levels also employed (0·8 and 0·6) were chosen so as to be similar to the apparent contrast expected to result from adaptation to a 1·0 contrast grating (Blakemore et al 1973).

5.1 *Method*

The transilluminated square-wave grating of 1·0 nominal contrast was prepared by attaching narrow strips of black tape to cellophane. The space-average luminance of this stimulus was 4·9 cd m^{-2}. The grating was viewed binocularly from a distance of 150 cm to give it a spatial frequency of 6·5 cycles deg^{-1} and a field size of 3 deg by 5·5 deg. The contrast of this grating was reduced to 0·8 by the superposition of a grey field (luminance, 1 cd m^{-2}) from a second field of the tachistoscope. The luminance of the grating was reduced to 3·9 cd m^{-2}, to maintain the stimulus luminance at 4·9 cd m^{-2}. The 0·6 contrast stimulus was obtained similarly. Persistence was measured, as for experiments 1, 2a, and 2b, by alternating the combined stimulus of grating and grey field with the blank.

The method of limits was used to determine the threshold for detection of the blank interval (Meyer et al 1975). Four threshold measurements were made in each block of trials. Two blocks of trials, presented in a counterbalanced order, were given for each contrast level. Eight subjects participated in the experiment. All were experienced observers, and the majority had participated previously in one or more of experiments 1, 2a, and 2b. A practice block of trials was given to each subject prior to commencement of the experimental blocks.

5.2 *Results*

Mean persistence, averaged over the eight subjects, was 285·3, 287·8, and 292·0 ms for the 1·0, 0·8, and 0·6 contrast levels respectively. The slight increase in persistence with decreasing contrast was not significant ($F_{2,14} = 0{\cdot}72$; $p > 0{\cdot}05$).

5.3 *Discussion*

The results of this experiment provided evidence that decreasing contrast does not result in decreased persistence under experimental conditions similar to those of Meyer et al (1975). In fact, a slight increase in persistence at lower contrasts was observed. Thus, the reduction in persistence as a result of orientation-specific adaptation (Meyer et al 1975; Meyer 1977) appears to occur as a result of a mechanism other than contrast reduction. This will be considered further in the general discussion.

6 General discussion

The main findings of the above experiments were that visual persistence increases with increasing spatial frequency, and that it decreases with increasing contrast. However, at high contrast levels, persistence appears to become independent of contrast, at least for low spatial frequencies.

The finding that the persistence of gratings increases with decreasing contrast may enable the effect of spatial frequency upon persistence to be partially explained by possible differences in the apparent contrast of gratings of different spatial frequency. A supplementary experiment was performed to test this possibility. Subjects matched the apparent contrast of 2, 4, and 8 cycles deg^{-1} gratings with a 0·44 contrast 16 cycles deg^{-1} grating. The persistence of this set of gratings matched for apparent contrast was then compared with that of 2, 4, 8, and 16 cycles deg^{-1} gratings of 0·44 contrast. The results, given in figure 3, show that the persistence of both the matched-contrast gratings and the 0·44 contrast gratings increased similarly with

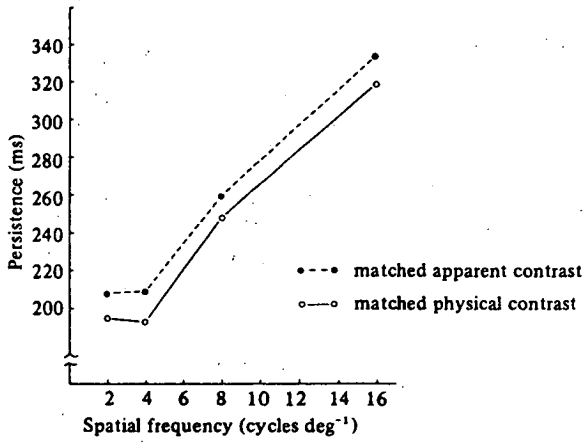

Figure 3. Mean persistence of gratings matched in apparent contrast and in physical contrast, as a function of spatial frequency.

spatial frequency. This indicates that the increase in persistence with spatial frequency is unlikely to be due to a reduction in the apparent contrast of high-frequency gratings. The apparent contrasts were, however, matched under steady viewing conditions, where only slight differences in contrast with spatial frequency were obtained (Georgeson and Sullivan 1975; Kulikowski 1976). The contrast matching may therefore not have been adequate under the experimental conditions.

The existence of afterimages may have a confounding effect on persistence as measured in these experiments. Subsequent observations have shown that this is true especially for long-duration stimuli (100–500 ms). In all the experiments reported in this paper, however, the stimulus duration was 50 ms, which does not give rise to negative afterimages at any contrast or spatial frequency (Corwin et al 1976). It is thus unlikely that afterimages would confound the present experiments[1].

The increase in persistence with spatial frequency is similar to the findings that both critical duration (Breitmeyer and Ganz 1977; Legge 1978) and duration of temporal summation (Watson and Nachmias 1977) are dependent upon spatial frequency. The close similarity between the effect of spatial frequency upon visual persistence and critical duration can be seen from a comparison of Legge's (1978) critical-duration data with the high-contrast-level persistence data from experiment 1 (figure 4). Both responses increase linearly with spatial frequency and the straight lines fitted to the data have similar slopes (regression coefficients were 13·2 for the persistence data, and 11·1 for the critical-duration data). The persistence values were considerably larger than the critical-duration data, as is generally the case in such comparisons (Ganz 1975).

It has been hypothesised that the dependence of both critical duration and the summation function upon spatial frequency are due to the different responsiveness of transient and sustained channels to varying spatial frequencies (Breitmeyer and Ganz 1977; Watson and Nachmias 1977). Since persistence appears to be related to these other temporal properties a similar mechanism may be responsible for the increase in persistence with spatial frequency. The finding that the persistence by spatial-frequency relationship is linear may be evidence for a gradual change from transient to sustained activity with increasing spatial frequency. This hypothesis requires a considerable degree of overlap in the spatial-frequency specificity of

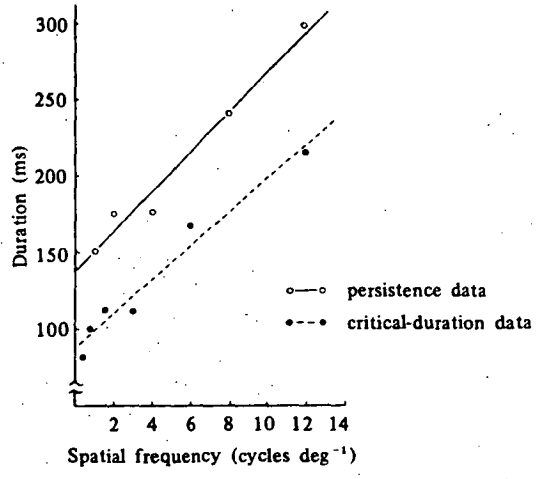

Figure 4. A comparison between the effects of spatial frequency upon persistence (data from experiment 1) and upon critical duration (data from Legge 1978).

[1] We are indebted to one of the referees of this paper for this suggestion.

sustained and transient mechanisms. There is some evidence of this in the data of Legge (1978), Tolhurst (1975a, 1975b), and Watson and Nachmias (1977). Using physiological procedures, Ikeda and Wright (1975) also discovered a considerable degree of overlap in the peak spatial-frequency sensitivity of cortical transient and sustained neurons in the cat.

It is also possible, however, that a spatial-frequency-dependent increase in the duration of sustained responses alone may occur (Breitmeyer and Ganz 1976). It is in fact possible that persistence at all spatial frequencies is due primarily to the prolonged responses of sustained channels, rather than to the activity of both transient and sustained channels. Under these circumstances, the activity of transient responses at the offset of a stimulus may have an inhibitory effect on the sustained response (Breitmeyer 1975a; Singer and Bedworth 1973), reducing persistence. Since transients are predominantly responsive to low spatial frequencies, powerful inhibition of the sustained response following stimulus offset would greatly reduce persistence at these spatial frequencies. At high spatial frequencies the effect of transient off-responses on sustained activity would be minimal. A combination of long-duration sustained responses and low transient activity may thus together account for the long persistences observed at high spatial frequencies. There is some evidence in the work of Eriksen and Collins (1967) for such a reduction in persistence as a result of 'off' responses.

This hypothesis may provide a tentative explanation of the contrast effect obtained in the current experiments. It is possible that a reduction in the activity of transient channels may have occurred in the current experimental situation when low-contrast gratings were employed (e.g. Harwerth and Levi 1978). As the gratings were alternated with a blank of the same space-average luminance, the small amplitude difference between the luminance profiles of the blank and grating may not have completely stimulated transient 'on' and 'off' activity, resulting in increased persistence. Greater transient activity producing decreased persistence would be expected to occur as contrast increased, until all transient mechanisms were fully activated (i.e. transient activity became saturated). Above this point, no further effect of contrast upon transient activity would be expected. Several studies confirm that motion-selective mechanisms, presumably transients, appear to saturate at low-contrast levels (Keck et al 1976; Pantle and Sekuler 1969; Pantle et al 1978).

Legge (1978) has shown that sustained activity occurs at spatial frequencies as low as 1 cycle deg^{-1}, and that this can account for the detection of grating signals in the absence of transient activity. Therefore, sustained activity persisting after the offset of low-contrast gratings as a result of the proposed reduction in transient off-responses may account for the increased persistence with decreased contrast observed at all spatial frequencies. Because transients are predominantly active at low spatial frequencies, increasing contrast would result in rapidly increasing transient activity and early saturation at these frequencies. This would result in the observed decline in persistence with increasing contrast tending to asymptote as contrast increased.

Although there appears to be little transient activity at high spatial frequencies, the ability to perceive flicker at higher-contrast levels of these frequencies (Kulikowski and Tolhurst 1973) is presumably an indication that transients do operate here. Stromeyer et al (1978) have also obtained evidence for the activity of movement-selective (transient) mechanisms at high spatial frequencies. Continuing to increase the contrast of high-spatial-frequency flickering stimuli may also increase the contribution of transient on- and off-responses. The continuing decline in the persistence of the 12 cycles deg^{-1} grating with increasing contrast may thus be attributed to a continually increasing proportion of off-responses producing greater inhibition of sustained activity. It would be necessary to conduct an experiment in

which the apparent contrast of high- and low-frequency alternating gratings was equated in order to assess the degree to which the difference in apparent contrast discussed earlier is important in this.

The possible effect of transient off-responses on persistence may also explain the adaptation results of Meyer et al (1975) and Meyer (1977). Adaptation to stationary high-contrast stimuli appears to have a disinhibiting effect upon transient activity (Georgeson 1976a, 1976b). This increased transient activity would presumably have a greater inhibitory effect on sustained activity (Singer and Bedworth 1973), resulting in decreased persistence. Further experiments are planned to investigate this possibility.

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Presence and absence of color selectivity in the motion aftereffect

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It is controversial whether the magnitude of the motion aftereffect is greater when both inspection and test stimuli are the same color rather than different colors (color selectivity). The present experiments show that the extent of color selectivity in the classical motion aftereffect depends upon (1) the duration of the interval between inspection and test, and (2) the nature of the stimulation during this interval. These findings are consistent with previous reports of two phases in the motion aftereffect and are interpreted in terms of the known properties of sustained and transient cells in the human visual system.

It has been demonstrated that the magnitude of the classical motion aftereffect is greater when both inspection and test stimuli are viewed in the same colored light than in different colored light under monoptic viewing conditions (Lovegrove, Over, & Broerse, 1972; Mayhew, 1975). With dichoptic viewing, the color relationship between the inspection and test stimuli has no effect on the magnitude of the aftereffect. These results were interpreted as indicating that at some level of the visual system there exist cells which are exclusively monocular and selective not only for direction of motion, but also for color (Lovegrove et al., 1972). A number of studies of contingent aftereffects in which subjects alternately view opposite color-motion combinations during inspection have also reported color selectivity in the motion aftereffect (Favreau, 1976; Favreau, Emerson, & Corballis, 1972; Mayhew, 1972, 1975; Mayhew & Anstis, 1972; Murch, 1974). In contrast, Day and Wade (1979) failed to demonstrate color selectivity in a series of experiments in which subjects viewed only one color-motion combination during inspection. They interpreted their results as evidence against the existence of color-motion detectors and for a distinction between classical and contingent aftereffects.

In a reply to Day and Wade (1979), Lovegrove, Over, and Broerse (1979) argued that the discrepant results might arise from the existence of two different phases in the motion aftereffect (Bonnet, Bouvier, & Petiteau, 1976; Bonnet & Pouthas, 1972; Favreau, 1976; Taylor, 1963).

Bonnet and Pouthas (1972) found that fast, vivid movement was visible on a noise background immediately following inspection of moving lines, but thereafter the aftereffect took the form of slower and less vivid movement which was seen best when the inspection and test stimuli were similar. In the first stage reported by Favreau, the motion aftereffect showed rapid decay and was sensitive to brightness-contrast but not to color, while in the second stage the aftereffect decayed slowly and was color-selective. In this case, color selectivity would depend on the duration of the interval between inspection and test, with Phase 1 effects normally being seen before Phase 2 effects. Lovegrove et al. (1979) also proposed that transient and sustained cells might underlie Phase 1 and Phase 2 aftereffects, respectively. There is both psychophysical and electrophysiological evidence that transient cells are relatively insensitive to spatial detail and lacking in color selectivity, whereas sustained cells exhibit spatial and color tuning (Dow & Gouras, 1973; Gouras, 1974; Tolhurst, 1977).

Day and Wade (1979) used a 1-sec interstimulus interval, thus possibly measuring Phase 1, whereas Lovegrove et al. (1972)[1] used a 15-sec interstimulus interval and possibly measured Phase 2. The present paper reports two experiments which support the above proposals.

Experiment 1, therefore, was conducted to determine whether the extent of color selectivity in the motion aftereffect depends on the duration of the interval between inspection and test.

EXPERIMENT 1

Method

Subjects. Twelve subjects with normal or corrected-to-normal vision participated in this experiment. All subjects were screened for abnormalities in color vision on the Ishihara test for color blindness.

Apparatus. The square-wave moving gratings used as inspection stimuli were produced by attaching black tape to a white belt which was driven by a small motor. The test pattern was produced by attaching black tape to white cardboard. The inspection and test patterns were presented in Fields 1 and 2 of a Scientific Prototype three-field tachistoscope (Model GB). An achromatic 1.1-cycle/deg square-wave grating print surround, subtending 9 × 9 deg with a Michelson contrast of .6 and space-average luminance of 4.4 cd/m², was presented in the third field of the

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tachistoscope. The circular inspection and test patterns both subtended 1 deg 44 min in diameter, had Michelson contrasts of .6, spatial frequencies of 1.1 cycles/deg, and space-average luminances of 1.1 cd/m². Both inspection and test stimuli could be displayed in red (Wratten filter 26; dominant wavelength 620.6 nm in illuminant A) and green (Wratten filter 55; dominant wavelength 524.1 nm in illuminant A) light. The Wratten filters were transilluminated by the tachistoscope light source. The grating moved from left to right at 2.5 cycles/sec.

Procedure. The general procedure followed that used by Lovegrove et al. (1972). Data were collected in four separate experimental sessions which followed one practice session. The five sessions were separated by at least 24 h. In any one session, the subjects adapted to only one color (initially for one period of 4 min and then for seven 1-min periods) and were tested in only one interstimulus interval conditon. Four measures of the motion aftereffect were taken on both the red and green targets following either a 1- or 15-sec interstimulus interval. Half of the subjects received the 1-sec delay condition first, and the other half the 15-sec delay condition first. Similarly, half the subjects adapted to moving gratings in green light first and the other half to red light first. Order of testing was randomized for each subject in a session, and viewing was monocular. The magnitude of the aftereffect was measured by subjects moving a pen laterally at the same apparent speed as the aftereffect. In the 1-sec interstimulus interval condition, the subjects continued to look at the patterned surround in the tachistoscope, whereas during the 15-sec interstimulus intervals they looked at a brick wall.

Results and Discussion

The mean magnitude of the aftereffect (mean pen displacement in 15 sec) for each color combination at interstimulus intervals of 1 and 15 sec is shown in Figures 1a and 1b.[2]

Since the data contained evidence for nonadditivity (inspection of the raw data indicated a strong interaction between subjects and conditions), a logarithmic transformation was applied before analysis in this and in the subsequent experiment. The analysis of variance showed that the difference between the 1- and 15-sec interstimulus interval conditions was significant [$F(1,11) = 10.86$, $p < .01$]. There was no significant effect of inspection color [$F(1,11) = 1.26$ $p > .05$] or test color [$F(1,11) = .25$, $p > .05$]. A significant inspection-test color interaction [$F(1,11) = 17.93$, $p < .01$] shows the presence of color selectivity. The three-way interstimulus interval-inspection-test color interaction was significant [$F(1,11) = 14.6$, $p < .01$], indicating a significant difference between the amount of color selectivity obtained with a 1- and 15-sec interstimulus interval. This experiment clearly shows that color selectivity in the motion aftereffect depends on the duration of the interval between inspection and test. Immediately after inspection, there is a strong motion aftereffect which is not color-selective. Fifteen seconds after inspection, the magnitude of the aftereffect is reduced and is dependent on the color relationship between inspection and test stimuli.

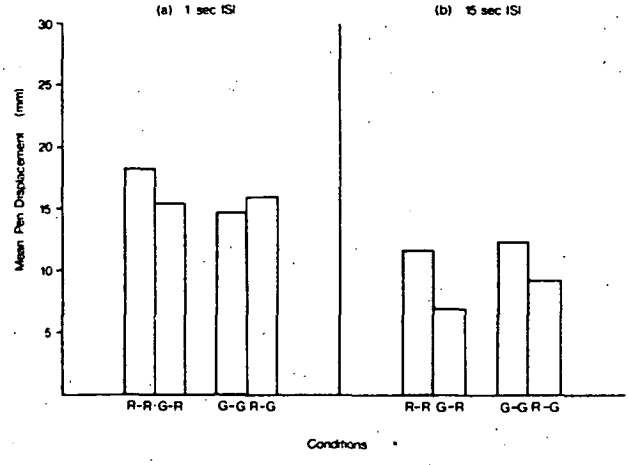

Figure 1. Mean magnitude of the motion aftereffect (mean pen displacement in 15 sec) with various combinations of inspection and test colors. In (a), the ISI was 1 sec, and in (b), the ISI was 15 sec.

EXPERIMENT 2

The preceding experiment suggests that color-contingent components of motion aftereffects, like pattern-contingent components, are not found until the initial phase has been dissipated. This dissipation may, however, depend on not only the presence of an interstimulus interval, but also the presence of stimulation during that period. The motion aftereffect is known to show little reduction when a dark period is interpolated between the inspection and the test periods Spigel, 1962; Wohlgemuth, 1911), and Bonnet et al. (1976) report storage of both noncontingent and pattern-contingent phases during relatively brief dark intervals. As subjects received patterned light stimulation during the 15-sec interstimulus interval in Experiment 1, the following experiment was conducted to determine whether this factor was important in demonstrating the contingent component.

Method

Subjects. Twelve subjects participated in this experiment.

Apparatus. The apparatus was the same as for Experiment 1, with one exception. During the 10-sec light interstimulus interval, a gray card covered by randomly positioned black dots and having a space-average luminance of 4.4 cd/m² was placed in the blank field of the tachistoscope.

Procedure. The procedure was similar to that of Experiment 1 in most respects. Two interstimulus interval conditions, both of 10 sec, were used. In the dark condition, the subjects looked into the completely darkened tachistoscope, whereas in the light condition, they viewed the random-dot card described above. In this experiment, the subjects tracked the apparent movement of the test stimulus for 10 sec rather than 15. The data were collected over four sessions. In any one session, the subjects adapted to only one color and tracked apparent movement on two test colors following either the dark or light interval. Presentation of conditions was counterbalanced across subjects.

Results

The mean magnitude of the aftereffect (mean pen displacement in 10 sec) for each color combination following light and dark intervals is shown in Figures 2a and 2b.

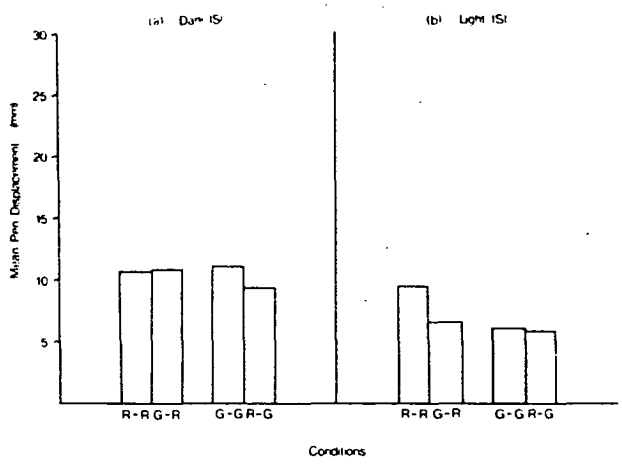

Figure 2. Mean magnitude of the motion aftereffect (mean pen displacement in 10 sec) with various combinations of inspection and test colors. In (a), the 10-sec ISI was dark, and in (b), the 10-sec ISI was bright.

An analysis of variance showed that the difference between the dark and light interstimulus interval conditions was significant [$F(1,11) = 12.00$ $p < .01$]. There was no main effect of inspection color [$F(1,11) = 1.16$, $p > .05$], but test color was barely significant [$F(1,11) = 4.92$, $p < .05$].[3] The presence of a significant inspection-test color interaction [$F(1,11) = 20.69$, $p < .001$] confirmed the existence of color selectivity. The three-way interaction was not significant [$F(1,11) = 2.53$, $p > .05$].

To clarify this situation, the data from the dark and the light interval conditions were analyzed separately. Under these circumstances, a strong inspection-test color interaction was still found for the light-interval data [$F(1,11) = 11.06$, $p < .01$], but there was no indication of any corresponding interaction for the dark-interval data [$F(1,11) = .004$, $p > .05$].

The results support the hypothesis that, in the absence of stimulation, the initial Phase 1 of the motion aftereffect will not be dissipated and will continue to obscure the later second phase. Informal observations suggest that, as would be expected from previous studies (Ross & Taylor, 1964; Spigel, 1962), higher luminance levels accelerate the dissipation of the initial phase. These factors may, however, be of importance only for relatively short interstimulus intervals. In reporting that both phases are stored to some degree during short periods of darkness, Bonnet et al. (1976) also noted that only the pattern-contingent phase was present after longer dark intervals. Supporting this are the results of a minor supplementary experiment with eight subjects, in which significant color selectivity was found after a 30-sec dark interstimulus interval [$F(1,7) = 9.50$, $p < .05$]. Due to the relatively informal circumstances under which this experiment was conducted (subjects were simply asked to close their eyes for 30 sec), it is, however, impossible to be certain that there was a total absence of retinal stimulation throughout the interstimulus interval.

DISCUSSION

The experiments reported here clearly demonstrate color-selectivity in the "classical" motion aftereffect. Color selectivity primarily depends on the duration of the interval between inspection and test.[4] In experimental conditions similar to those used by Day and Wade (1979), there was no evidence that the motion aftereffect is color selective. Experimental conditions using an interstimulus interval similar to that used by Lovegrove et al. (1972) did demonstrate color selectivity. The latter depends, however, on the nature of the stimulation during this delay. This evidence supports earlier proposals of two distinct phases in the motion aftereffect, with the first phase not demonstrating color selectivity while the second phase does. It is argued that Phase 1 effects result from adaptation of transient cells whereas Phase 2 effects result from adaptation of sustained cells.

The theoretical and methodological considerations raised in this paper have relevance beyond the original issue of the conditions under which color selectivity in the motion aftereffect occurs. First, these considerations are likely to be of equal relevance to the study of *any* contingent components in the motion aftereffect. Second, if the identification of the two phases of the motion aftereffect with the sustained and transient systems is correct, their relative strengths will be altered by manipulating variables such as rate of motion and contrast which differentially affect the two systems (Keck, Palella, & Pantle, 1976; Pantle, Lehmkuhle, & Caudill, 1978). Third, even though there may be a number of ways to distinguish classical from contingent motion aftereffects, the presence or absence of color selectivity is not one of these. Rather, there are two ways of inducing motion aftereffects; inspection of a single color-motion stimulus as used in this paper and alternate inspection of opposite color-motion combinations (Favreau, Emerson, & Corballis, 1972). The former induces a motion aftereffect with both a simple and a contingent component, whereas the latter has only contingent components.

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NOTES

1. Neither Lovegrove et al. (1972) nor Day and Wade (1979) specified the interstimulus interval duration used in their experiments.

2. The absolute magnitude of the aftereffects measured in this experiment is smaller than that reported by Lovegrove et al. (1972). It is, however, the relative magnitude of the aftereffect under same and different color conditions rather than absolute aftereffect magnitudes which is crucial to the argument presented in this paper.

3. This significant target-color effect appears to have resulted from the small aftereffect seen in the green-green condition by one subject. In this condition, 9 out of the 12 subjects experienced more aftereffect on the green-green than on the red-green condition. Two of the remaining subjects experienced slight reversals, whereas the third subject experienced such a large reversal that his "reverse" color selectivity was equal to the total color selectivity experienced by the other 9 subjects.

4. In further experimentation, using 1-, 5-, and 15-sec interstimulus intervals, the dependence of color selectivity on interstimulus interval duration was even more clearly demonstrated. The 1-sec condition produced no color selectivity, the 5-sec condition produced color selectivity on one test stimulus color only, and the 15-sec condition produced color selectivity on both test stimulus colors.

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The effect of stimulus duration on the persistence of gratings

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The persistence of gratings varying in spatial frequency and exposure duration was measured using a stimulus-blank alternation method. Persistence was found to lengthen with increasing spatial frequency and to shorten with increasing exposure duration. For each spatial frequency, persistence decreased linearly with a slope of approximately −.75 as duration increased for short stimulus durations. For longer stimulus durations, the rate of decline in persistence with increasing duration was reduced, the slope being approximately −.13. The stimulus duration at which the change in slope of the persistence-duration relationship occurred was shown to increase with increasing spatial frequency and was approximately equivalent to the critical duration for each spatial frequency. The data were consistent with an interpretation of persistence in terms of a temporal integration component and a second, possibly cortically located, component.

It has been shown, in a range of experimental situations, that the visual response to a stimulus frequently outlasts the actual duration of the stimulus (Efron, 1970a; Haber & Standing, 1969, 1970; Sperling, 1960). This continuation of a response after the offset of a stimulus is known as visual persistence (Briggs & Kinsbourne, 1972) or visual information store (Meyer, Lawson, & Cohen, 1975). Persistence, which appears to result from neurological activity in the retina and/or visual cortex is influenced by stimulus variables in a manner similar to other temporal and spatial properties of the visual system. Its duration is increased by decreased adaptation level (Haber & Standing, 1969, 1970), luminance (Bowen, Pola, & Matin, 1974; Efron, 1970b), and contrast (Bowling, Lovegrove, & Mapperson, 1979). Persistence duration is also lengthened by increasing the spatial frequency of grating stimuli (Bowling et al., 1979; Meyer & Maguire, 1977) and by decreasing the duration of the stimulus (Efron, 1970a, 1970b; Haber & Standing, 1970). The relationship between the effects of the duration and spatial frequency of gratings upon persistence was the subject of this investigation.

Haber and Standing (1970) found that the persistence of a letter array stimulus declined with increasing stimulus duration, decreasing to nearly zero for stimulus durations longer than 350 msec. Efron (1970a, 1970b) obtained a similar result with a low-intensity (8.8 cd/m^2) colored circular field on a dark background. In all of these experiments, the total apparent duration of the stimulus remained constant for stimulus durations ranging from near 0 to over 100 msec. For durations within this range, the duration of persistence decreased linearly with a slope of −1.0 as stimulus duration increased. Once the duration of the stimulus exceeded 100-200 msec, however, either negligible persistence was observed (Efron, 1970b) or the duration of persistence remained constant with increasing stimulus duration (Efron, 1970). The stimulus duration at which the change of slope in the persistence by duration relationship occurred was called the "critical duration" and was estimated to be about 130 msec (Efron, 1970a, 1970b). The data of Haber and Standing (1970), with a letter array stimulus and light pre- and postadapting fields, indicate that the critical duration is approximately 200 msec under these conditions.

Data obtained by Di Lollo (1977) and Di Lollo and Wilson (1978) also indicate that an inverse relationship between persistence and stimulus duration exists for stimulus durations up to 100-130 msec when the stimuli are light pulses presented on a dark background. The stimulus durations for which this relationship holds are similar to the durations over which time-intensity reciprocity (Bloch's law) occurs under low illumination. The critical duration over which temporal integration occurs is approximately 100 msec under this condition (Barlow, 1958; Roufs, 1972). It is hypothesized that the inverse relationship between stimulus duration and persistence is due to the limited temporal resolution of the visual system, the response to a brief stimulus persisting because it is "smeared" over the period of temporal integration of the visual system. Consequently, at least one component of persistence may be identified with temporal integration. Further evidence for this identification may be obtained from the observation that variables which affect integration time affect persistence similarly. The durations of both temporal integration and persistence increase with decreasing illumination (Bowen et al., 1974; Efron, 1970b; Roufs, 1972) and with increasing spatial frequency of grating stimuli (Breitmeyer & Ganz, 1977; Bowling et al., 1979; Legge, 1978; Meyer & Maguire, 1977).

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Many measures of persistence duration indicate that this is often considerably longer than the critical duration (Bowling et al., 1979; Haber & Standing, 1969, 1970), presumably indicating that factors other than integration time may contribute to persistence. Appreciable persistence may also be observed for stimulus durations exceeding the critical duration under some circumstances (Efron, 1970a). A second persistence component, which possibly occurs at the cortical level, is hypothesized to exist in addition to temporal integration at the periphery (Breitmeyer & Ganz, 1976; Eriksen & Schultz, 1978). There is some evidence that cortical elements are involved in persistence (Haber & Standing, 1969; Meyer, 1977; Meyer et al., 1975).

These hypotheses may be tested by investigating the effect of stimulus duration on persistence under circumstances in which the integration time of the stimuli can be manipulated. This can be done by varying the spatial frequency of gratings, since the critical duration increases with increasing spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978). It was hypothesized that the stimulus durations at the change in the slope of the persistence by duration relationships would be similar to the critical durations and increase with increasing spatial frequency. The persistences of gratings varying in spatial frequency and exposure duration were consequently measured. Two linear regression lines were fitted to the data for each spatial frequency, and the points of intersection of these lines were observed for each spatial frequency. The stimulus durations at which the point of intersection occurred (critical duration) were consistent with threshold measures of critical duration, increasing with spatial frequency.

METHOD

Apparatus

The stimuli were presented by means of a Scientific Prototype three-channel tachistoscope (Model GB). The stimuli were three photographic reproductions of oscilloscope-generated sinusoidal gratings subtending spatial frequencies 1, 4, and 12 cycles/deg. The contrast of all gratings was estimated to be .44 from a plot of Michelson contrast against the output level of the oscilloscope (in volts). The space-average luminance of the gratings and of the blank with which they alternated was kept constant at 9 cd/m^2.

Subjects

Twelve subjects were used. These were volunteers, predominantly postgraduate students and staff of the Psychology Department. Several had participated previously in similar experiments, but the task was new to a number of subjects. All had normal, or corrected-to-normal, vision.

Procedure

Persistence was measured in the same manner as described by Bowling et al. (1979). The grating stimulus was alternated with a blank interstimulus interval (ISI) for 10 cycles. The duration of the ISI was varied in 10- or 20-msec steps, and the subjects were asked to report whether a distinct blank interval was visible between each grating cycle. A double random staircase method was employed (Cornsweet, 1962). For each block of trials, the initial ISIs of the ascending and descending staircases were chosen so that they were 100 msec apart. The blank was not visible at the initial ISI of the ascending staircase and was clearly visible at the initial ISI of the descending staircase. A few initial trials were generally necessary to establish these starting points. Six threshold reversals were obtained in each block of trials.

A total of 18 blocks of trials, each of which comprised one stimulus condition, was performed on each subject. Each stimulus condition comprised one of the three spatial frequencies (1, 4, anc 12 cycles/deg) at one of six durations (50, 75, 100, 150, 200, 300 msec). Two experimental sessions of approximately 1 h duration were employed. An initial practice block of trials preceded the experimental blocks in each session. The order of presentation of the stimulus conditions was randomized, with the constraint that conditions involving each spatial frequency be separated from each other by conditions involving the other two spatial frequencies. This was to minimize possible adaptation effects.

RESULTS

The data are shown in Figure 1. For each spatial frequency, a decline in persistence was observed with increasing stimulus duration. The analysis of variance indicated that the main effect of duration was highly significant [$F(5,55) = 17.08$, $p < .001$]. A highly significant spatial frequency effect was also observed [$F(2,22) = 56.64$, $p < .001$]. Longer persistence was observed with increased spatial frequency at all stimulus durations. A significant Spatial Frequency by Duration interaction [$F(10,110) = 3.02$, $p < .01$] indicated that the rate of decline of persistence with increasing duration differed across spatial frequencies. Two linear regression lines were fitted to the data for each spatial frequency by the method of least squares. The stimulus durations and persistence values of the points of intersection of the two lines were obtained.

These values, together with the slopes of the regression lines, are given in Table 1. There is some variation between the slopes with different spatial frequencies (see Figure 1), but these do not appear to follow a regular pattern. The mean initial slope over the three spatial frequencies was $-.75$, and the mean secondary slope was $-.13$. The values of critical duration derived as indicated in Figure 1 were plotted against spatial frequency (Figure 2). A linear relationship between critical duration and spatial frequency with a slope of 8.3 was obtained.

Table 1
The Slopes of the Linear Regression Lines Fitted to the Data and the Stimulus Durations at the Points of Intersection (Critical Durations, in Milliseconds) for Each Spatial Frequency (in Cycles/Degree)

Spatial Frequency	Slope		Critical Duration
	Initial	Secondary	
1	−.62	−.14	60
4	−.89	−.09	88
12	−.74	−.16	152

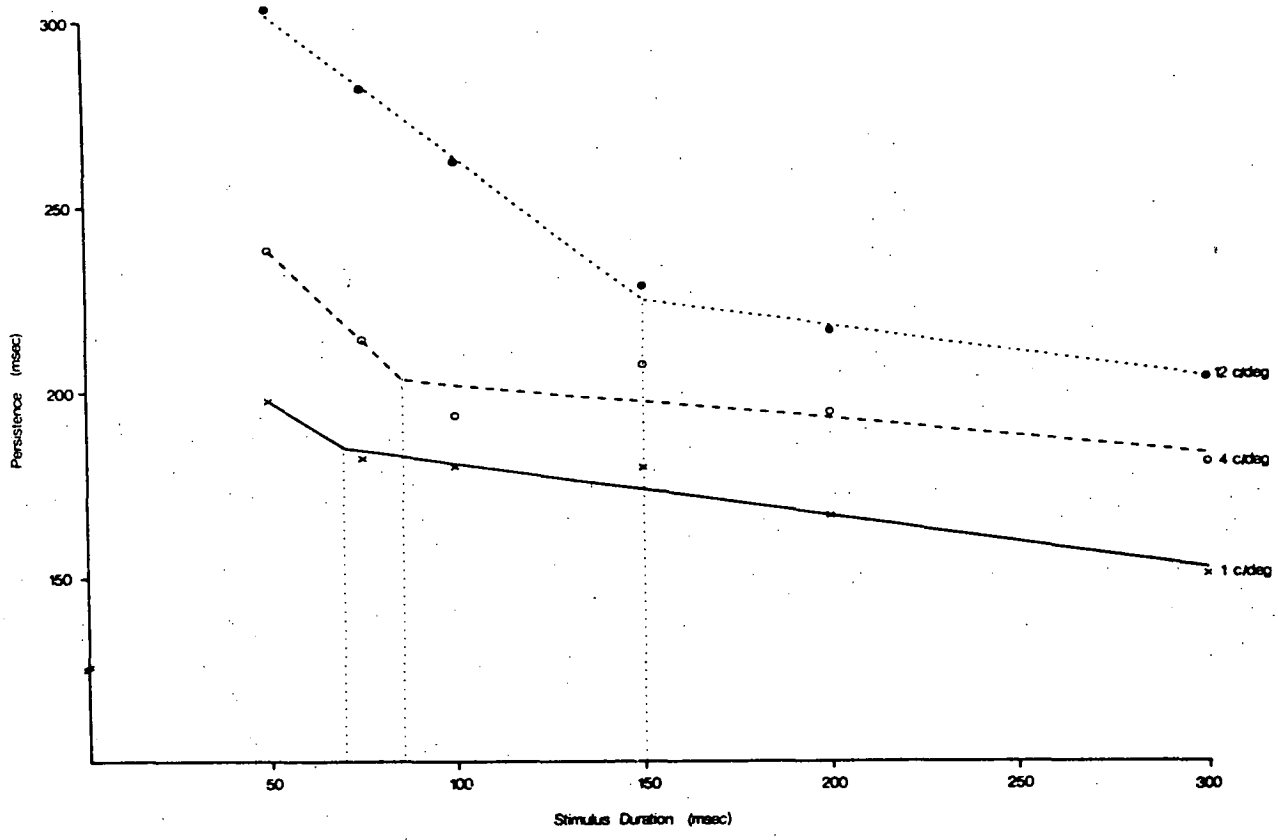

Figure 1. The relationship between stimulus duration and persistence for gratings of spatial frequencies of 1, 4, and 12 cycles/deg. The critical duration is obtained from the points of intersection of the two regression lines.

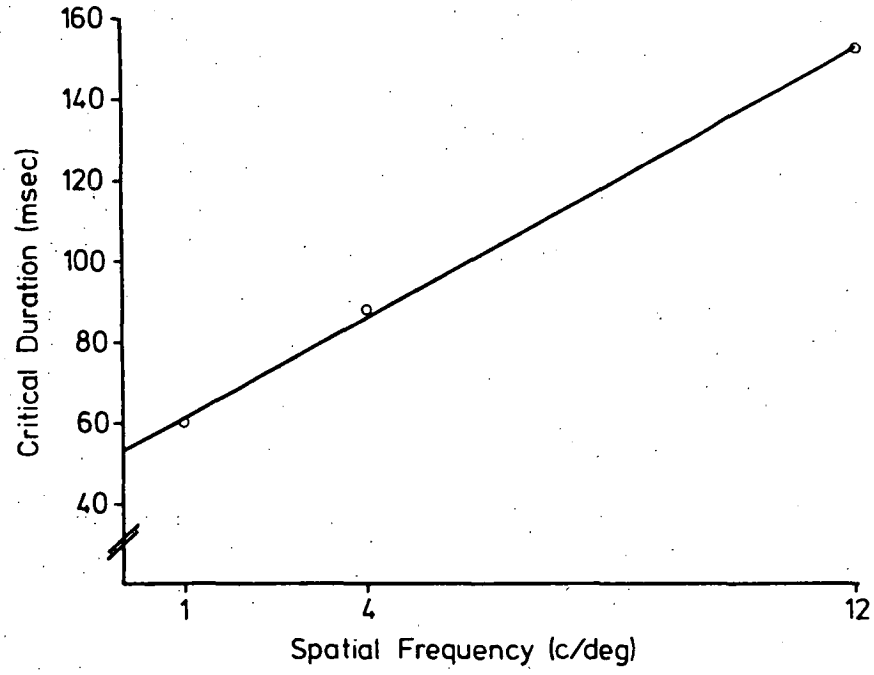

Figure 2. The stimulus durations of the points of intersection of the two regression lines describing the persistence-duration relationships, plotted against the spatial frequency of the gratings.

DISCUSSION

The data indicate that the persistence of gratings of short exposure duration declines linearly with increasing stimulus duration for each spatial frequency investigated. For long stimulus durations, there was only a shallow decline in persistence with increasing duration. This is consistent with the data of Efron (1970a) and Haber and Standing (1970). The stimulus duration at which the change in slope occurred (the critical duration) was found to increase linearly with increasing spatial frequency (see Figure 2). This increase with increasing spatial frequency is similar to the observed increase in threshold measures of critical duration with increasing spatial frequency (Breitmeyer & Ganz, 1977; Legge, 1978), although the values for critical duration derived in this experiment are somewhat shorter than Legge's (1978) values. Critical duration is known to vary with other stimulus conditions such as luminance (e.g., Roufs, 1972) and may differ for threshold and suprathreshold measurements and for monocular and binocular viewing conditions (Ueno, 1977). Thus, the observed differences between the values of critical duration obtained by Legge (1978) and the values for the stimulus duration at the change of slope do not necessarily invalidate the identification of the latter with critical duration. In addition, it is not claimed that these values represent accurate measures of critical duration under the conditions of the experiment, being only approximate estimates of the duration of temporal integration for the three spatial frequencies employed.

The results of this experiment have indicated that persistence duration is dependent to some extent upon the integration time of the visual system and consequently increases under conditions where the critical duration is increased. The increased persistence of high-frequency gratings observed in this and previous studies (Bowling et al., 1979; Meyer & Maguire, 1977) may thus be partly due to the increased integration times of gratings of these frequencies. The increase in persistence with increased spatial frequency cannot be entirely attributed to longer integration times, however, since this relationship is also observed when the stimulus durations are considerably longer than the integration times of all three spatial frequencies (see Figure 1).

Further evidence that persistence is dependent upon spatial frequency at long stimulus durations can be obtained from a study by Corfield, Frosdick, and Campbell (1978). These authors used techniques similar to those used in this study to measure persistence and showed that "grey-out elimination" increased with increasing spatial frequency for exposure durations of 600-900 msec. The existence of substantial persistence at long durations may be interpreted as indicating that, using the method of measurement reported in this paper, an additional factor (or factors) may contribute to visual persistence apart from temporal integration. Not all methods of measurement of persistence, however, provide evidence for this factor. For example, Haber and Standing (1970), who used a different technique, found that persistence was virtually zero for long-duration stimuli. In addition, methods of measuring persistence that involve integration of two or more successive stimuli do not provide any evidence for a second component (e.g., Di Lollo, 1977; Di Lollo & Wilson, 1978). It is possible that the characteristics of the second component differ from those of the integration component and that the second component is therefore not detected by all experimental methods. It may originate at later stages of the visual system, possibly as a result of the prolonged activity of sustained cells at the cortical level (Breitmeyer & Ganz, 1976).

Under the conditions of this experiment, the slope of the initial decline in persistence with increasing stimulus duration was found to be approximately $-.75$, instead of -1.0 as expected. This result may have been due to the method of measurement employed, since different subjects tended to adopt very different criteria for detection of the blank ISI. Subjects who indicated that they could identify the blank interval at short ISIs generally showed smaller effects of stimulus duration than subjects who identified blanks at considerably longer ISIs. A supplementary experiment, in which the same procedure was carried out using repeated sessions with a single subject (who adopted a long ISI criterion) indicated that, under these conditions, the initial slope was much closer to -1.0.

The slope of $-.75$ obtained in this experiment may also possibly be explained by comparison with the results of the temporal integration experiments of Breitmeyer and Ganz (1977) and Legge (1978). In each of these investigations, it was found that perfect temporal integration does not occur when the contrast detection thresholds of grating stimuli are measured. The initial slope of the Log Contrast by Log Duration relationship in these experiments was found to be approximately $-.70$ rather than -1.0. The relationship between stimulus and contrast at threshold is thus $C \times (t)^{.70} = k$ (Breitmeyer & Ganz, 1977) rather than $C \times t = k$ (Bloch's law). This would cause integration of short-duration stimuli to take place over a shorter period of time than the long-duration stimulu, resulting in the relationship obtained in this experiment. The slope of $-.75$ may thus be due to imperfect temporal integration occurring under the conditions of the experiment.

The results described by this paper are generally in agreement with those obtained by previous investigators when the persistence of stimuli varying in duration was measured. They support the hypothesis that many investigations of persistence apparently include two separate persistence components in the measurement and that the first of these components may be identified

with temporal integration. The nature of the second persistence component has not yet been ascertained, apart from the possibility that it originates in the visual cortex (Meyer, 1977; Meyer et al., 1975).

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Specific Reading Disability: Differences in Contrast Sensitivity as a Function of Spatial Frequency

Abstract. *Contrast thresholds for sine-wave gratings of spatial frequencies of 2, 4, 12, and 16 cycles per degree were determined for normal and disabled readers at a range of stimulus durations. Normal readers demonstrated monotonically decreasing sensitivity with increasing spatial frequency at exposure durations between 40 and 100 milliseconds. At exposure durations of 150 to 1000 milliseconds, they showed peak sensitivity at 4 cycles per degree. In comparison, disabled readers showed monotonically decreasing sensitivity with increasing spatial frequency at all stimulus durations. The difference in sensitivity pattern across spatial frequencies was greatest at stimulus durations approximately equal to fixation durations during reading.*

A long and controversial research history concerns possible visual factors in specific reading disability (*1*). While numerous reports (*2*) have shown no differences between good and poor readers in spatial perception, more recent studies have indicated that the two groups differ in terms of their spatio-temporal processing (*3*). This conflict may relate to methods of assessing visual capacity. Specifically, although clinical patients with problems in pattern perception and reading have normal visual acuity, they have more subtle visual deficits that become evident when vision is assessed by determining the contrast sensitivity function (*4*). We have now demonstrated that normal and disabled readers differ in the pattern of sensitivity across spatial frequencies and that this difference depends on stimulus duration. At short stimulus durations, both groups showed a monotonic decrease in sensitivity with increased spatial frequency. With longer stimulus durations, especially those which approximate reading fixation durations, normal readers were most sensitive at 4 cycles per degree, whereas disabled readers continued to show a monotonic decrease in sensitivity. Comparison of the two groups in terms of critical duration as a function of spatial frequency reveals no significant differences. This result indicates that the visual persistence differences mediated by spatial frequency that have been reported between good and poor readers (*5*) are likely to be cortical and not retinal in origin.

A stimulus property fundamental to the processing of spatial information is spatial frequency measured in terms of the number of cycles of a sine-wave grating per degree of visual angle. Recent physiological (*6*) and psychophysical (*7*) research has indicated that different spatial stimuli may be processed in separate channels rather than in a single channel. The contrast sensitivity function, a measure of visual performance across all spatial channels, has useful clinical applications (*8*) in situations in which normal acuity tasks have proved inadequate. Individual channels process only a limited range of spatial frequencies and differ in temporal properties measured by reaction time (*9*), critical duration (*10*), and visual persistence (*11*). There seem to be two components to visual persistence (*12*), only the second of which, influenced by grating orientation and contrast, is presumably cortical (*13*). The first component has properties similar to temporal integration and may result from such integration. Stimuli shorter than the critical duration may consequently measure both components, whereas longer stimuli measure only the second component.

The slope of the function relating visual persistence to spatial frequency is significantly flatter in disabled than in normal readers (*5*). Because persistence was measured with stimuli of short duration, there was no indication of the persistence component on which normal and disabled readers differed. We therefore compared normal and disabled readers in terms of the contrast sensitivity function at a range of stimulus durations. In addition to revealing subtle visual deficits concealed by standard optical assessments, this method also provides a measure of temporal integration (retinal persistence) at each spatial frequency.

Contrast thresholds for reading-disabled and control subjects were obtained for sinusoidal gratings of 2, 4, 12, and 16 cycles per degree at stimulus exposure durations of 40, 60, 80, 100, 150, 200, 300, 500, and 1000 msec. Two groups of ten 14-year-old boys matched in intelligence (*14*) and socioeconomic status were tested. The disabled readers had average intelligence and an average reading age lag of 5 years on the Neale Analysis of Reading Ability (*15*), showed no gross behavioral problems, and suffered from no organic disorders. Both groups had 6/6 Snellen acuity or better.

A 2° (diameter) sine-wave grating display (space-averaged luminance of 2.2 cd/m^2) was presented on a cathode-ray tube (B.W.D. model 539D, ^{31}P phosphor). Either a target (grating) or catch (blank) trial was initiated when the subject pressed a button. Subjects were required to report the presence or absence of the grating on each trial.

Contrast thresholds were determined according to the blockwise tracking procedure (*16*). Each block consisted of 12 trials—six target trials and six catch trials. In succeeding blocks, contrast was either increased or decreased from the starting contrast, previously determined by preliminary testing to be close to threshold. Testing continued until subjects achieved 75 percent accuracy in any one block or bracketed 75 percent accuracy between any two successive blocks. The presentation order for spatial frequency and duration was counterbalanced. Each subject was tested in at least two sessions. Viewing was binocular throughout.

The control data are consistent with data previously reported for adults (*10*), showing a monotonic decrease in sensitivity with increase in spatial frequency (from 2 to 16 cycles per degree) at short durations (40 to 100 msec) (Fig. 1). With longer durations, control subjects began to show peak sensitivity at 4 cycles per degree.

Only at the longest duration used (1000 msec) did disabled readers begin to show a sensitivity peak at 4 cycles per degree. Analysis of variance revealed that a significant ($P < .05$) or near significant ($P < .10$) groups-by-frequency interaction for the quadratic trend (*17*) occurred for all stimulus durations from 150 to 500 msec. Thus, the sensitivity pattern differences (Fig. 1) are significant. The pattern in the two groups did not differ with the 1000-msec stimulus duration. These analyses consequently show that, for stimulus durations similar to fixation durations in reading, normal and disabled readers have considerable differences in the shapes of their contrast sensitivity functions.

The relative miss and false-alarm rates for the two groups were compared by Mann-Whitney *U* tests, which revealed no differences between the groups. It is unlikely, then, that these results are produced by differences in criterion setting between the two groups.

Critical durations for each subject (*18*) under each condition were obtained by standard procedures (*13*). Because of the correlation between the means and variances for each condition, a logarithmic transformation was applied to the raw data before analysis. There were no significant differences between the two groups [$F(1, 18) = 2.5$, $P > .05$]. The significant effect of spatial frequency

[$F(3, 54) = 7.0$, $P < .01$] showed that critical duration increased with spatial frequency in 14-year-olds as well as in adults (*10*). There was not a significant interaction between reading ability and spatial frequency [$F(3, 54) = 1.4$, $P > .05$].

In terms of the two-component theory of visual persistence (*13*), it can be concluded that the frequency-mediated differences in visual persistence between normal and disabled readers at ages 8 (*5*) and 14 (*19*) years do not result from differences in the retinal component. Presumably the difference arises at the cortical level. There are two further sources of evidence for this conclusion. Contrast, which influences cortical but not retinal persistence (*13*), influences persistence differently in disabled and normal readers (*19*). In addition, the pattern of persistence in normal and disabled readers across spatial frequencies differs most when stimuli of long duration (*19*) are used to measure the cortical component. How differences in visual persistence mediated by spatial frequency may influence reading has been discussed elsewhere (*11*, *19*).

The different patterns of contrast sensitivity between the two groups may be compared with those reported by Bodis-Wollner (*4*). He reported that adult clinical patients with altered sensitivity to limited spatial frequency ranges experienced difficulty in pattern perception and reading. Recovery of normal sensitivity after treatment was accompanied by the return of normal pattern recognition and reading ability. The selective losses in spatial frequency sensitivity in some of his subjects resembles that reported here for disabled readers at intermediate stimulus durations.

Our analysis indicates that disabled readers should experience a general visual deficit on many integration tasks. Difficulties in reading should be only one manifestation of the problem. Because the differences in sensitivity patterns between the two groups are greatest with stimulus durations approximately equal to reading fixation durations, the problems may be maximized in reading. That disabled readers do have a more general spatio-temporal problem is shown in a recent study (*20*) requiring subjects to identify pictorial and verbal material moved behind a stationary slit (*21*). Disabled readers had more difficulty than control subjects with both sorts of stimuli, a result indicating a general deficit in spatio-temporal integration. It is possible that the differences reported here underlie such difficulties.

The contrast sensitivity differences between the groups reported here differentiated the individuals in each group almost without exception (*22*). Consequently, this measure may provide an easy means of screening young children for potential reading problems before they begin to read. Furthermore, the results merit consideration in terms of constant claims that normal and disabled readers do not differ visually (*2*) and, consequently, that remediation approaches should concentrate on "intact visual abilities" (*23*).

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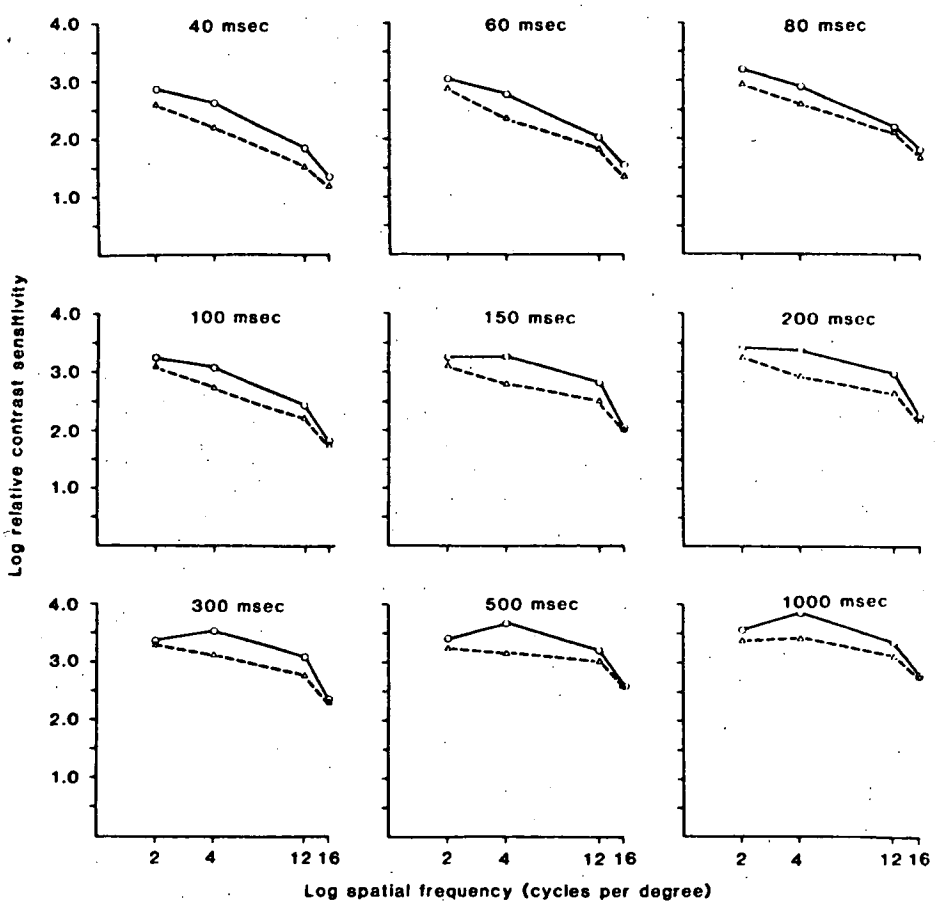

Fig. 1. Contrast sensitivity functions as a function of stimulus duration for the reading-disabled (△) and the control (○) groups.

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